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hoped, through such a course, to bring specialists into mutually helpful and stimulating relations with one another, and at the same time to make their work and thought intelligible and useful to beginners.

It was not intended to take the place of systematic lectures, such as are given in the regular courses of instruction; it stands rather for the higher and the more general needs of the science. Its leading purpose, if I may be permitted to define it more with reference to the possibilities of its future development than to its present attainment, was to meet the rapidly growing need of co-operative union among specialists. Specialization has now reached a point where such union appears to be an essential means of progress. Specialization is not science, but merely the method of science. For the sake of greater concentration of effort, we divide the labor; but this division of the labor leads to interdependence among the laborers, and makes social co-ordination more and more essential. This is the law of progress throughout the social as well as the organic world. An organism travels towards its most perfect state in proportion as its component cell-individuals reach the limit of specialization, and form a whole of mutually dependent parts. Scientific organization obeys the same law. As methods of investigation improve, specialization advances, and at the same time the mutual dependence of specialists increases. Isolation in work becomes more and more unendurable. Comparison of results, interchange of views and ideas, and a thousand other advantages of social contact, become of paramount importance to the highest development.

is an organism, the biologist declares that an organism is a society.

A society is an organized whole, the unity of which consists in, and is measured by, the mutual dependence of its members. The living body is an organization of individual cells with the same bond of unity. The principle of organization in both cases is the division of labor or function. The primitive social aggregate—the undifferentiated germ of society—is composed of practically like units, with like simple needs. Every one is a *factotum*, fulfilling all needs in and for himself. It is all self-dependence and no mutual dependence. The coherence of the whole is so slight that it can break up into as many parts as there are individuals, without the sacrifice of a single tie or condition essential to existence.

In course of time, division of labor comes into play, and with it social organization has its beginning. The different members, instead of doing all sorts of work, and aiming only to supply their own individual wants, begin to limit themselves to such work as their tastes, capacities, surroundings, etc., commend to them. This concentration of effort, which Coleridge, in his theory of life, has defined as “the tendency to individuation,” both strengthens and improves the productive power, thus enabling a few to do the work of many. Each class of specializers produce in excess of their own needs, and through the exchange of these surplus products the needs of all are supplied.

The social integration that accompanies such division of labor may best be seen under conditions conceived as simple as possible. Let it be assumed that we have

its chief distinction from a purely gregarious aggregate.

If the members of such a community, in adaptation to the conditions it imposes, should become so far differentiated as to lose the power of providing for more than one or two of the ten necessities of existence, the social unity would become as inviolable as the physiological unity of the higher organisms. Break it, and every member would soon perish, just as certainly as every cell would die if the body were irreparably injured. The social organism might endure the loss of a limited number of its members, as the animal organism survives the death of individual cells and even the loss of certain organs. These losses may be repaired, in the one case by substitution, in the other by regeneration.

If reparation fails, all the remaining parts suffer in proportion to their dependence on the parts lost. In either case, the more complete the division of labor, broadly speaking, the more perfect becomes the unity of parts, the more complete the coincidence of the individual with the general welfare.

The parallel is more complete than our assumed case is suited to illustrate. We have considered only the two extremes of a series, and have not allowed for any connection through intermediate stages of development. But division of labor is not an artificial affair arbitrarily fashioned to our convenience ; it is not a thing of human device, for it antedates both the written and the unwritten history of our race. In the organic world, its development has been as slow and as long as the rise of the beings now inhabiting the earth ; in the human

Our knowledge, so far as it goes, points to the conclusion that division of labor is not only co-extensive with life, but also coeval with it. Indeed, we should be on the side of all the probabilities, in assuming that the simplest possible form of living matter presupposes this principle. We are not, of course, to confound the principle with life itself, nor with the cause of life ; it is only a condition or means to an end. The universal correlate of division of labor is union of the laborers. It always means specialization, and always implies organization.

Thus the paradox resolves itself. As Herbert Spencer long ago pointed out in his *Social Statics*, "progress is toward complete separateness and complete union," and "the highest individuation is joined with the greatest mutual dependence."

As you see, the principle is one which may re-inaugurate itself, as often as a new order of units is evolved with needs that can be most economically and efficiently served by a co-operative union. We do not know how many times this may have happened before the cell order of beings arose ; but the general course of development following this stage, we are now very confident about.

Some of these cells, finding independent nomadic life congenial, have persistently declined every temptation to part with individual freedom. They have kept their freedom, but with it the low estate of unaided individual effort. Precious freedom that, which excludes all those larger possibilities of life which we see unfolded in the organic world.

Others preferred company to isolation, and herded

of the colony. Neither class can dispense with the services of the other ; and this dependence of part upon part gives the colony a certain physiological unity. But the integration of the colony is of such a simple order, that we might conceive it splitting up into as many independent colonies as it contains times the least number of cells of both sorts necessary to maintain the physiological connexion. Although in practice, we could not carry the division so far, still we know that artificial, if not spontaneous, division would be possible without destroying the physiological unity necessary to the continued existence of the severed parts.

One feature of labor-division in *Volvox* deserves mention here, chiefly as foreshadowing more complex conditions seen in higher forms. It is the alternation of agamic with gamic generation. The agamic reproductive cells are all alike, and correspond to parthenogenetic ova ; while the gamic generation is represented by two distinct kinds of cells answering to ova and spermatozoa, and conjugation is necessary to development.

This alternation of parthenogenesis with hermaphroditic gamogenesis — is not, we may be sure, an acquisition of the colony ; it is rather to be regarded as a combination of features that originated separately and successively among the unicellular ancestors of the colony. Parthenogenesis must have been the primitive mode of reproduction ; gamogenesis undoubtedly originated secondarily in adaptation to infusorial conditions of life.

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workers, uniting in such intimate fellowship as to constitute an indissoluble whole — a real conscious intelligent unity — with powers so far transcending those of its units that we can form no conception of the special combinations from which they result, — when we contemplate this miracle of co-adjustments among myriads of units, among these systems of units, and these systems of systems, we are not disposed to ridicule the judgment that once refused to believe that natural forces could produce such wonders, and took refuge from the difficulties that beset every mechanical theory in the doctrine of preformation.

If our microscopical aids have enabled us to know that organisms are not simple unfoldings of pre-existing structures, and have revealed the fact that every developing germ actually re-enacts the wonders of a new creation, still it is no less an unscrutable mystery than before. Indeed one must credit the preformationists with having perceived and emphasized the real difficulty in the way of any rational theory of generation. We endeavor to meet it, by assuming, not pre-existing rudiments, but pre-existing hereditary units; not predelineations, but potentialities, of structure. Predeterminations of some kind or other are a logical necessity, and so there is some analogy between our position and that of Bonnet, Haller, and Cuvier, and other evolutionists of the old school, although we are compelled to regard the process of development as one of epigenesis, as conceived by Aristotle, Harvey, John Hunter, and Casper Friedrich Wolff. The difference between the two schools reduces itself to the difference between potentialities and actualities; and although the difference as understood

which characterizes the Hydra stage. In correlation with this important step, we have one grand and several minor structural features introduced. The digestive cells arrange themselves together in the form of a tubular sack open at one end, thus taking the first step towards a rudimentary alimentary canal. Around this sack, the remaining cells station themselves, forming another sack inclosing the first. The sacks are in close contact, and the walls of the outer one are continuous with those of the inner one at its open end, so that the inner sack may be regarded as an infolding, such as we might rudely represent by pushing in the end of a glove-finger. If the material were elastic, so that we could draw out the double wall around the open end into a number of arm-like extensions, we should have a fair model of the Hydra body with its tentacles.

The cells constituting the inner sack, called the entoderm, are in the most favorable situation for attending to the food-supply of the entire cell community; and natural selection has constrained them to specialize in this direction until they have become inoperative in other ways, and even incapable of doing anything else. Trembley succeeded in turning these creatures inside out; and as they lived on after such treatment, he inferred that the functional differentiation of the two layers was so slight that ectoderm and entoderm could exchange places and works. The mistake has only recently been corrected by a Japanese naturalist. Dr. Ischikawa of Tokyo has shown conclusively that Hydra cannot live long turned inside out, and that, if left to itself after the operation, it soon turns itself back into its normal condition. This act of recovery escaped the

The remarkable thing about such an individuality is, that a hundred of them may be added together and the sum total will be but one; and yet you may divide this *one* into a hundred *ones*.

Mr. Ischikawa succeeded in forcing two individuals into complete and permanent coalescence; and for aught we can see, the experiment might be repeated indefinitely. One Hydra was turned inside out, and then pushed into the mouth of another until the digestive sacks of both were brought together one within the other. A bristle was then thrust transversely through both bodies to prevent separation. In the course of a few days, the two bodies were completely merged in one, and the resulting individual was a perfect personal unity, bearing two sets of tentacles as the only mark of its double origin.

Having seen in what the essential unity of Hydra consists, we can readily understand why such an individuality may not be weakened by division or strengthened by doubling. A society of a hundred individuals with ten labors, distributed as we supposed, would represent a unity with ten essential points of union. Now we could double the number of members without increasing the points of union; and we could divide the whole community into ten communities, each with as complete a functional unity as that of all combined.

In the case of Hydra, we could divide more freely, because the points of union are fewer. Now what I wish to emphasize here is this: *The more the points of union multiply in a social or an organic body, the more complex and extended becomes the integration of its parts, and the less susceptible it is to such divisions and fusions*

dividing it more or less equally among many cells, scattered or grouped according to the nature of the work. Nature is provident as well as bounteous, and so she determines the number of workers not only with reference to ordinary needs, but also with a view to emergencies. The cell cannot work on indefinitely. Exhaustion follows exertion; rest and recuperation are as necessary to the cell as to an individual; hence the need of relays. The cell has its own term of existence, which is usually much shorter than that of the organism; hence the need of substitutes. So each class of specialized cells may greatly exceed in number the actual needs of the moment. One of the best illustrations of this fact is seen in the reproductive cells, which are often so enormously in excess of use, that they are scattered in the water or the wind, with not one chance in a thousand of ever fulfilling the purpose of their existence. All such profuseness, however, has its meaning, even though it only neutralize accident, and so insure a few the realization of their proper destiny.

But these hosts of cells suffice for only one of the many varieties of reproductive work. They are called reproductive cells, not to indicate monopoly of the entire work, but pre-eminence merely in one important branch of it. Propagation of the species is their task; but this becomes a monopoly only among the higher forms of life. The same work may be accomplished by budding and fission, processes which prevail very largely among plants and many of the lower animals, usually supplemented, however, by the more general process of reproduction by means of specialized cells.

But the generation of the species, which follows such

cells, etc., are replaced by deeper and younger cells, called "intermedial." The reproductive cells have the same origin.

The work of reproduction then is not confined to any one or two classes of cells; it is divided and subdivided in endless detail, carried all through the organism, and distributed independently of most other labors. Its elaboration in this or that direction may be correlated with a system of morphological differentiations, so extensive and involved that a whole course of lectures would be required to elucidate the subject. Take the genital system of the vertebrates, or that of forms no higher than the annelids, and you will find no end of problems yet to be settled. What complicated cycles of generation have been followed by many parasitic forms, especially among the worms, and what wholesale modifications of structure in answer thereto. How devious have been the paths of generation in insects, and how wonderful the metamorphoses attending them. How diverse the ways of multiplication among the Tunicates and Coelenterates, and what puzzling successions and combinations of forms have here tried the sagacity of naturalists.

What peculiar corporation aggregates are represented in Siphonophore colonies, of which we have a most beautiful example in the Portuguese-man-of-war. How long it has taken to decide between the "poly-organ theory" of Eschscholtz, Huxley, Müller, and Metschnikoff, and the "poly-person theory" of Vogt, Leuckart, Kölliker, Gegenbaur, and Haeckel. The complex of reproductive processes in one such colony would still bear a life-time of research, and not be

which merges their individualities into an individuality of a higher order. The tendency towards unity, as specialization advances is nowhere more strikingly illustrated than in the progress from the lower to the higher segmented animals. In the lower annulose types, the individual represents a chain of segments or somites, which we may regard as so many individuals which have arisen as buds, one after the other, from before backwards, but have remained connected in the order of origin. These somites retain their individuality to such an extent that they are not killed by artificial separation, and indeed often undergo spontaneous fission.

As we glance along the line of forms terminating in the Myriopods, the Crustaceans, the Insects, and the Arachnids, we find the individualities of the somites more and more subordinated to that of the chain they compose. There is a progressive consolidation, which, in its extreme phases, more or less completely obliterates the traces of articulation. The illustration might be extended to the vertebrates, but that would be needless. Let me add only, as one of the broadest conclusions to be drawn from such facts as we have been considering, that *the grade of specialization attained in any group of organisms determines its rank in the scale of life and intelligence.*

In each order of units, specialization seems to have its limit in the highest possible integration of its component elements. When this limit is reached, progress is arrested. The only way then open for advance lies in combining these units into units of a higher order. In this combination is given the possibility of a

in turn has its limits in our power to improve the methods of investigation. The tendency, then, is regulated by the necessities and advantages of the investigator; and although we may not be able to fix definite limits to its growth, we are not the less certain that it has such limits, and that there is no danger either of a wholesale reaction or of our ever specializing to pieces. As in the organic and social worlds, so in the scientific, there are centripetal forces that keep pace with the centrifugal ones; and the danger of any science flying into disconnected atoms is about as dreamy and remote as the dissolution of the earth itself.

The movement in the direction of separation is general and, as it *now* seems to us, rapid. Cuvier thought that division of labor characterized the natural science of his day; but the movement was then in its earliest infancy. If you wish to know how extensive it has now become, you should look at the ponderous volumes of the "Zoological Record" or the "Naples Jahresbericht." When you reflect that it requires such massive volumes to record the bare titles and a brief abstract of the work of a single year, you realize how impossible it is for any one naturalist to cover the whole ground, or even to read the hundredth part of what his collaborators have to report.

Naturalists then are no longer cosmogonists, but specialists. This being the fact, what is to be done in view of it? Where lies the remedy for every danger of narrowness that may lurk in the tendency to specialize? How is the range of vision to be kept free and broad while focussing attention on some one point of the field? If one specialty absorbs our whole

journals as the *Zoölogischer Anzeiger*, the *Biologisches Centralblatt*, the *Anatomischer Anzeiger*, the *Journal of the Royal Mic. Soc.*, the *Zeitschrift f. wis. Mikroskopie*, &c. Manifestly all such specialization is led by the coöperative spirit.

But it is not to the general tendency so much as to our own special need that I would now direct attention. We have now reached a point where our advance, both individually and collectively, depends, far more than ever before, upon the privileges, the opportunities, and the many peculiar advantages inherent in the principle of coöperative work.

Among the ways of bringing together our scattered forces into something like organic union, the most important, and the most urgent at this moment, is that of a national marine biological station. Such an establishment, with a strong endowment, is unquestionably *the* great desideratum of American biology. There is no other means that would bring together so large a number of the leading naturalists of the country, and at the same time place them in such intimate helpful relations to one another. The larger the number of specialists working together, the more completely is the organized whole represented, and the greater and the more numerous the mutual advantages.

Just consider what such an organization implies. It means, first of all, a permanent staff of investigators, with laboratories equipped for special research, and with facilities for extending observation to different points of our varied coast. It means boats, and all needful appliances for collecting, dredging, etc. It means a corps of trained collectors at the service of the investigators.

be effected through the unaided effort of any one person. But individual effort, though weak alone, has in the growing aggregate a cumulative power that often surprises expectation. Let every one feel, therefore, that his or her personal interest in the matter may be just what is required to make the combined effort of all effective in converting possibilities into actual realizations, and in giving to specialization its consummation in organization.

logical research is in the direction of a *genealogical* system of classification—a system based upon, and expressing, the kinship which underlies the whole organic world. From this standpoint, the myriad forms of organisms that have arisen since the dawn of life, genealogically arranged and viewed as a whole, would present the branching figure of a tree. The trunk and branches of this great tree, representing ancestral forms, have been buried in the sand and mud of geologic ages, and preserved only as an imperfect fossil frame-work, so that we see only the terminal buds of its topmost twigs in the plants and animals of to-day. To trace out and reconstruct such a tree is a work of magnitude, scarcely dreamed of in the philosophy of cabinet naturalists. The best classification within the range of present possibilities can only have a tentative value. It can have not a single hour's security against the invasion of newly discovered facts—an invasion that is advancing along a thousand lines with plenary authority to spare nothing fictitious. The goal of systematic botany and zoology is not then the terminus of any one line of research, but rather a focal point of all the biological sciences.

Having noted the principal aim of classification, we have now to glance at its position, scope, and functions. The low standards followed by many systematic writers have brought reproach upon this department of knowledge; but the reproach is certainly misplaced, and we must accord to systematic biology the high position to which its true aims and functions entitle it. Its first business, obviously, is to ascertain what forms of life now exist, and to describe, name, and catalogue them

enunciated, the awe-stricken recipient retires, feeling profoundly edified, and credits his informer with having fulfilled the function of a great naturalist. This mischievous delusion is too often encouraged by those who are able and willing to impose upon it, or who have not the courage to follow the injunction so often given by Professor Agassiz at Penikese, — "Learn to say you do not know."

Pitiable as is this fear of appearing ignorant, and despicable as is the impostor's pretence of knowledge, there is no ground in either for prejudice against systematic names.

Whoever reflects on what the binary nomenclature, introduced by Linné, has done for zoology and botany, will scarcely need to be told that no misuses, excesses, or abuses to which systematic work is liable, can detract from its importance. Indeed, it may be said that time will increase rather than diminish the value of such work. Thirty years ago our systematic names stood for differences and resemblances, the deeper significance of which had only been caught by Darwin and Wallace. The idea of the genetic unity of the organic world set the whole field of systematic work in a blaze of light, imparting to it an interest and a dignity of the highest order.

The second important function of systematic biology is to arrange its forms in a genealogical system. But for the fulfilment of this function, systematic biology requires the aid of all the sister branches of knowledge, and in return renders the important service of recording their verdicts along with its own. The record, representing as nearly as possible the consensus of all the mor-

what the bond of unity actually lies. He would have no conception of what Huxley has called "the physical basis of life," and the structural unit of all organisms would lie wholly beyond the range of his perception. That isthmus of small life between the animal and vegetable kingdoms, his unaided vision would never discover. In searching for intermediate forms, he would inevitably be led astray by those deceptive appearances under which adaptive development and degeneration have concealed so many ancestral relationships. Sessile animals, like the sponges, the hydroid polyps, the sea-anemones, the polyzoa or moss polyps, the ascidians, and many others from the higher as well as the lower classes, would be separated from animals having the power of locomotion, and be regarded either as plants, or as forms representing both plants and animals. Where immobility is combined with the branching form, as in the hydroid polyps, the disguise would be complete. Even Linné, the great lawgiver in systematic biology, described such forms in the tenth edition of his "*Systema Naturæ*" as "plants with animal flowers"; and in the twelfth edition, which concluded his systematic work, he held to the opinion that the stock of the hydroid colony is a true plant, while its "flowers" are true animals. This idea was embodied in the word *zöophytes*, plant-animals, a word that has done varied service in systematic zoology from the middle of the 16th century.

The utter insufficiency of external characters as a guide to genetic affinity, is well seen when we come to such forms as the so-called compound ascidians, which are found encrusting the rocks along the shore. At first sight one would not even detect any signs of life here,

Thus you see how far from the surface the truth may lie, and how, in the systematic position of a single form, we may find a problem which only yields to solution after exhausting the resources of nearly every department of animal biology.

In order to correct and extend the results of surface observation, the investigator appeals first to internal structure, and is thus led into the province of anatomy. Here fundamental features of relationship are brought more clearly into view; and, following the general law that animals or plants of like structure have descended from common ancestors, it becomes possible to outline, in a rough way, a genealogical system. It is here that the investigator would begin to grasp the meaning of those deeper resemblances, called homologies, and learn to distinguish between these and deceptive analogies. But nature has concealed many of her more important homologies under disguises that a study of adult structure could not penetrate. Comparative anatomy, in the hands of such men as George Cuvier, Friedrich Meckel, Johannes Müller, Richard Owen, Thomas Huxley, and Carl Gegenbaur, has accomplished wonders in this direction, but it owes many of its greatest discoveries to the aid of embryology and paleontology. Its greatest achievement was the reduction of the animal world to four great types, and the same high elevation was reached independently by comparative embryology.

But the type system of George Cuvier and Carl Ernst von Baer did not finish the reconstruction of the genealogical tree; for it failed to grasp the full meaning of like development and like structure. Comparative anatomy

in their adult condition, if they pass through closely similar embryonic stages, we may feel assured that they are all descended from one parent-form." Thus embryology came to have a higher value in classification than anatomy, and to take the place assigned to it by v. Baer more than half a century ago, as "the true torch-bearer in the investigation of organic bodies."

Embryology and paleontology have become complementary sciences, associated in the common aim of determining the genesis and the history of life. The peculiar charm of embryology is, that it brings us into direct contact with living forms, places us face to face with the phenomena of life, and reveals in the history of the individual the principal events in the history of the race. It holds the key to many a problem that has exhausted the resources of all the sister branches of biology, and promises to contribute more than all the rest towards the solution of the great mystery of life.

In order to illustrate the relative position of embryology, and at the same time the nature of the naturalist's work, let us now look at one of the problems before him.

II. *A Special Problem.*

Naturalists are familiar with the efforts of comparative anatomy to determine the number of segments in the vertebrate head. At the beginning of this century, Germany's great poet, Goethe, and one of her most gifted naturalists, Oken, came independently to the idea that the skull is only an enlarged and otherwise modified portion of the backbone ; that is, that it is composed of

vertebrate characters is in the lower rather than the higher forms, and in the embryos rather than in the adults. The original expounders of the vertebral theory pursued just the opposite course, and were thus deceived by superficial analogies.

This theory, wide of the mark as it was in its original form, contains a germ of truth, which embryology has brought to light. Its fundamental idea, that the head, in whole or in part, is composed of segments morphologically equivalent to those of the body, may now be said to be an established fact. The problem as it now stands is this, — How far is the segmentation of the body carried forward into the head? in other words, how many segments are represented in the head? Let us look a little further into the nature of the problem, and the methods and means of approaching its solution.

The subject is a difficult one to make intelligible to those who are not familiar with the main features of development; but it is so full of instruction, that it cannot fail to yield some points of interest even to a most superficial examination. Possibly the idea of segmentation of the head, or, to use the technical expression, the metamerism of the head, may appear to some of you quite devoid of general interest or importance. The principal charm of the subject of course lies in its environment, if I may use such a term, to express its general relations or bearings. In attempting to decipher the metamerism of the vertebrate head, we are really engaged in tracing the history of the origin of the great vertebrate stock or phylum. It is simply a question of the genesis or the *phylogeny* of the vertebrate type,

stem, which bears the deep and enduring mark of metamerism.

So much for the general significance of metamerism. Let us now return to the vertebrate head. If the metamerate type of structure precedes and forms the foundation of the vertebrate type, then the question how many primordial segments are represented in the head takes precedence of the question how many vertebræ compose the skull. The inquiry takes us back to that interesting stage in which the embryo becomes divided into a chain of segments. But here we find that the transverse lines marking the boundaries of the segments do not extend into the region of the head, or at most only into its hinder portion. But we are not yet satisfied that the head is a thing *sui generis*, built upon a plan fundamentally different from that of the body. Baffled in the attempt to find *direct* evidence sufficient to demonstrate the unity of plan which we suspect underlies both the head and the trunk, we next resort to indirect or circumstantial evidence, and begin to question whether the records of ancestral development have been perfectly preserved in the embryonic development. It is here that the towering difficulties of the problem come into view, in scaling which investigation rises to its sublimest heights.

Before the division into segments, there is nothing in the embryo to show even approximately where the head ends and the body begins; the part which is destined to become the head forms with the rest a continuous whole, as shown in the external form and in the continuity of like structural elements. The cordal axis before alluded to is the precursor of the backbone, and

an eligible witness to the metamerism of the vertebrate head.

We are indebted mainly to recent studies on the development of the nervous system for the views now held on this subject. In the trunk we find each segment provided with a pair of so-called spinal nerves, both of which spring from the spinal cord by two short roots, known as the anterior and the posterior root. The posterior root bears, just before its union with the anterior root, a spinal ganglion, and is thus stamped as something different from its fellow. This anatomical distinction is the basis of a physiological distinction, the discovery of which, by Sir Charles Bell, in the early part of this century, has been regarded as the most important acquisition of physiology since the time of Harvey. Bell determined by experiment that the posterior roots are appointed for sensory, the anterior roots for motor, work. Thus both structure and function suggest that the spinal nerve is not *one* nerve, but two nerves united; and this point is settled beyond dispute, first, by the independent and unlike development of the two roots, and second, by their complete and permanent separation in such fishes as *Amphioxus* and *Petromyzon*. Each segment of the trunk may therefore be said to have two pairs of nerves, a sensory pair with ganglia, and a motor pair without ganglia.

Now we come to a question of absorbing interest not only to the embryologist but also to the anatomist and physiologist. Are the metameric arrangement, the division of labor or function, and the mode of development, essentially the same for the cranial as the spinal nerves? The several inquiries into which the question resolves

I must now invite you to the very borders of the beaten ground of investigation; and I hope you will have the fortitude to follow me even to the brink of a precipice or two, should it be necessary, in order to get a view of the steep ascent which now challenges further advance in this direction. I have endeavored to give you the salient points in the historical development of the subject, and it remains for me to define the position now occupied, and so far as possible, by way of anticipation, the path which investigation is destined to take in the immediate future.

In the anterior region of the head, into which the cordal axis or "primitive backbone," as Lankester has called it, does not extend, there are two sensory nerves, the olfactory and the optic, which investigation has thus far failed to reduce to the type of the spinal nerves. No corresponding motor nerves exist; and no decisive evidence of metamerism has yet been discovered in their development, or adult condition. Foremost authorities in anatomy and embryology, like Gegenbaur, Balfour, and Kölliker, have declared that here a dividing line must be drawn, separating the head into two distinct regions, one of which bears with the trunk the common stamp of metamerism, while the other is built upon a plan of its own. It is here that Balfour, looking back into the remote ancestral history of the vertebrates for clues, recognized what appeared to him a primitive boundary line, corresponding to what now divides the head and trunk in many invertebrate forms. According to this view, the fore-brain would represent the *whole* of the ancestral brain, while the mid-brain and hind-brain - would represent a number of segments belonging origi-

in the skull, the primordial cranium, the cranial nerves, the head-cavities, or the gill-clefts, nor, in short, in any one organ or system of organs that could be named in the head. As Professor Dohrn has insisted, both by word and example, nothing less than a complete analysis of the whole head and trunk can furnish a safe foundation for speculation on this subject. But the task does not end with the vertebrates. The present vertebrate head represents the cumulative development of unnumbered æons, and its ancestral history is only very imperfectly recorded in its embryonic development. Our analysis must therefore be extended to the worms, the arthropods, the molluscs, and, as it now appears, even to the coelenterates. The history of metamerism must be traced upwards, and the lessons of the simpler types must be our stepping-stones to a knowledge of the higher.

There is little prospect of ever knowing precisely how many segments the ancestor of the vertebrates possessed. The number varies in the different branches of a common stock; and we know that this variation is the result of loss in many cases, and suspect that it may be due to addition in others. But we know that this variability in number has very definite limitations in the laws that control the formation of segments. The possibilities in this respect are by no means the same for all regions of the segmented axis. Although the head segments have undergone the greatest modifications in form, *fixity in number is here the rule*, while variation, if we except degenerate forms, is confined to the posterior trunk segments. In the embryo the anterior segments are invariably first in formation,

until at last, stripped of one disguise after another, they have been almost, if not quite, reduced to the level of the sensory nerves of the trunk and hind head, through the researches of Marshall, His, Beard, and others. The identification of this pair of nerves with the rest of the segmental sensory nerves, on the basis of development and structural features, is a triumph of investigation so near at hand that it is scarcely premature to proclaim it. The chain of discoveries bearing on this subject has still many links to be supplied, and here is one of the opportunities of the hour.

The optic nerves still hold undisputed possession of the very pinnacle of isolation; and even to question their claim to such a position may appear to betray a woful superabundance of speculative audacity that would be less unbecoming to a romancing visionary than to the sober investigator. But without hesitation or misgivings, and without any special claim to scientific prevision, I venture to predict that these nerves and their sense-organs will yet fall into line with the other sense-nerves and sense-organs.

I cannot here enter very far into the question of the origin of the vertebrate eyes, but the subject is one of such great interest, that, at the risk of overtaxing your forbearance, I venture to ask your indulgence for a few general remarks. The evidence in favor of the derivation of the organs of the special senses from a common basis, has been growing during the past few years with such astonishing rapidity, that the hypothesis of independent origin has no longer a respectable claim to attention. If the eyes have been derived from some simpler form of sense-organs possessed by the ancestors

almost incredible that cells devoted to one of these functions could ever serve the other. Nevertheless, this marvellous transformation and change of function have actually taken place, and the fact still admits of ocular demonstration in a very large group of annelids. Sometimes all the tactile cells are converted into visual cells; at other times only a part of the cells assume the new function, while the rest continue to serve the old. The result is that we have at one end of the series pure visual organs, at the other end pure tactile organs, and between the two extremes every grade of mixture represented in veritable compound sense-organs. The picture is a revelation that gives swift wings to suggestion. If such is the path of evolution in one case, the best ground is given for suspecting that the same economy has been practised elsewhere. The discovery of these facts in the leeches, led naturally to the anticipation of a similar origin for the eyes in other annelids and in those groups that have had a common origin with the annelids, before all the arthropods and vertebrates. The existence of segmental sense-organs, as I have said, is well known in other annelids than the leeches, and the origin of eyes from them is fairly well indicated in many cases. It is a most promising subject of investigation, which, like a thousand others, still waits for the encouragement which the wealth of this country will not long, I trust, refuse to supply.

The close relationship between the annelids and arthropods rendered it probable that in the latter the eyes were also derived from segmental sense-organs, and the probability was strengthened by the arrangement of the eyes in successive pairs, as in the larvæ of many insects.

with a special problem and found it to be the centre of inquiries, leading in all directions into the unknown. So it is with all special subjects in biology. The farther we pursue them the broader and more interesting they become. Nothing could be farther from the truth than the idea that such questions are isolated, and devoid of interest to all except the specialist.

Of the numberless genealogical inquiries raised by the theory of organic evolution, none has a higher interest or has attracted more general attention than the derivation of vertebrates, involving, as it does, the origin of all the highest manifestations of vital structure and action. So long as the evolution theory remained an unproved and comparatively vague hypothesis, as it was left by Lamarck and St. Hilaire sixty years ago, the origin of vertebrates, like other genealogical inquiries, could have no more than a speculative interest, and could produce little direct effect upon morphological investigation — which indeed had quite enough to take care of at home, without following speculative zoology in her erratic excursions. When, however, the field of action had been cleared by such pioneers as von Baer, Johannes Müller, Remak, and Kowalevsky, when speculative zoology had been redeemed and vitalized by Darwin, and the theory of organic descent established on a firm footing, morphological research entered upon a new phase. A broad foundation of known facts had been laid; a splendid working hypothesis had been found. The central question in every morphological investigation became two-fold; it was no longer simply *what is?* it was also *how came it to be?* And this second question, be it observed, is not properly a speculative matter at all, but an historical one; it relates not to an ideal or hypothetical mode of origin, but to a real process that has actually taken place in the past and is to be determined like any other historical event. “Speculative zoology” thus, by slow degrees, became the guide and leader of research, and every morphological inquiry became, in the last analysis, a genealogical one.

the fact that growth takes place mainly at one end (the posterior) of the embryo, differentiation becoming more marked as we proceed forwards along the antero-posterior axis of the body. For the sake of brevity, this may be called *apical* or *unipolar* growth. To these fundamental morphological peculiarities we may add a third — that in all vertebrates the body appears to be built up, in a greater or less degree, by the union along the median line of parts that are laid down in the embryo as separate bilateral foundations. This I shall term *conrescence*.¹ Vertebrate morphology therefore presents three fundamental problems for solution, viz., the origin of (1) metamerism, (2) apical growth, and (3) conrescence; and these three lie at the root of all others.

Let us now turn to the invertebrate types. Do any of these possess the three characteristics in question? There are two such types, namely, the *arthropods* (insects, arachnids, crustacea, etc.) and the *annelids* (earthworms, leeches, and a great number of marine worms). The arthropods may, however, be left aside, since the annelids are in every respect simpler and less specialized, and there is strong reason to believe that the leading features of arthropods are inherited from annelid-like ancestors. The annelids have a typical metamerism and they are the lowest of segmented animals; apical growth appears among them in its clearest and simplest form; the phenomena of conrescence are nowhere so

¹ The term is here used in a wider sense than is ordinarily employed. The occurrence of conrescence in the more restricted sense among the vertebrates is not generally admitted to be a fact, and very eminent authority can be cited both for and against it. However, this very division of opinion in regard to so deep-lying a question only serves to render its investigation more interesting and important.

brates indicate real affinity, then the trochophore larva must be taken to represent, in a certain sense, the ancestor of all the higher forms of life. According to a

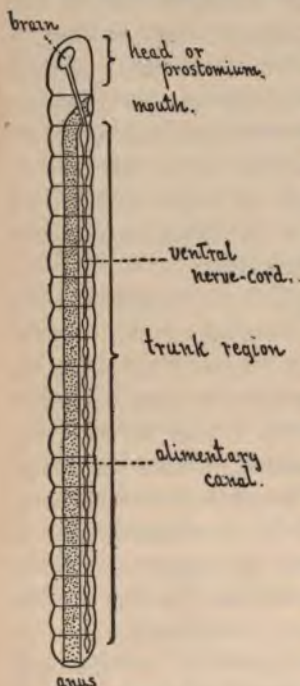


FIG. 1.

in my opinion, render the annelids, and particularly their trochophore larvæ, worthy of especial attention; and which give value to the investigation of every detail of their morphology. We turn now to a more special account of the annelids.

The body of an annelid (Fig. 1, which may be taken

a second school, however, the trochophore has no such remarkable significance, but is a "secondary" or "adaptive" larval form — *i.e.*, one secondarily interpolated into the development and representing no ancestral group; as is the case, for example, with the larvæ of insects. Whichever view be taken, a precise knowledge of the trochophore is essential to the investigation of the general problems indicated; and I shall show further on that the study of this remarkable larva raises a number of very singular questions regarding the nature and origin of the higher forms of life.

I trust that this introduction will suffice to make clear the general considerations which,

nation of body to head in studying the development of an annelid.

Upon this simple plan all annelids are constructed, though they are almost as varied in the details of their organization as the vertebrates themselves. The head may be provided with the most elaborate lobes, tentacles, cirrhi, branchiæ, eyes, etc. ; or it may lose all of these special organs and become reduced to an insignificant rudiment, as in the earthworm. The trunk is no less diversified ; sometimes a simple jointed cylinder, sometimes provided with lateral appendages of the most diverse character in different forms and performing many functions—locomotion of many varieties, respiration, sensation, etc.

Let us now turn to the development ; I select *Polygordius*, a form generally regarded as one of the sim-

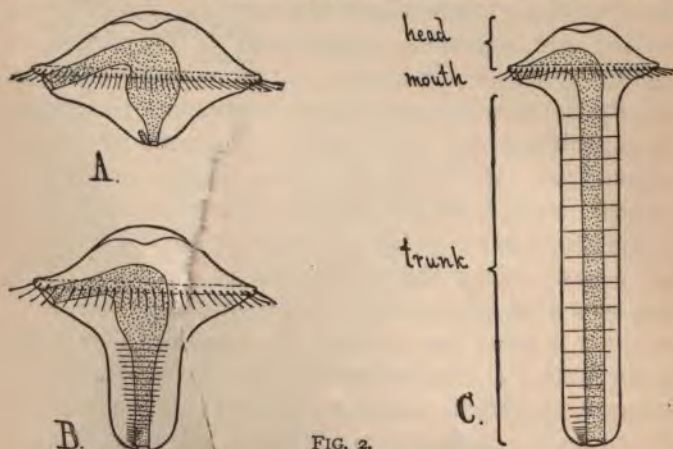


FIG. 2.

plest and most primitive of the annelids. *Polygordius* has a perfectly typical trochophore larva (Fig. 2), shaped

described further on. The newly formed trunk ultimately becomes so large that the original substance of the trochophore forms the head only,¹ which is in *Polygordius* scarcely larger than one of the trunk-segments. The cilia of the prototroch disappear, the animal sinks to the bottom, burrows into the sand, and assumes the adult condition.

Let us examine the significance of these facts. It appears that the head is the oldest part of the body, and that in a certain sense the trunk is its offspring, — as a branch is an offshoot from a tree. In other words, the egg develops into what we may regard as a free-swimming head, and this after a while buds off the body—an afterthought, as it were. Observe now the genealogical question that is at once raised. If this mode of development be in any manner a repetition or representation of the ancestral development, then the ancestors of the annelids, and of all the higher metameric types, are represented to-day in the head. And the head must, therefore, be historically, as well as embryologically, the oldest part of the body, and the trunk is a later acquisition.²

We may go farther than this. The trunk, I have

¹ This statement demands some qualification, since the extreme lower pole of the larva, bearing the anus, is carried down with the growth of the trunk, and remains as the so-called telson of the adult. It is, however, unnecessary to complicate the discussion by bringing in this fact.

² The "head" of arthropods and vertebrates probably represents the prostomium plus a certain number of trunk somites, closely united and devoted to special functions. Indeed, these somites have so far usurped the functions of the original prostomium that it is doubtful whether this can any longer be distinguished in the arthropod or vertebrate embryo. This, however, does not affect the essence of the historical question under consideration.

to include the genealogy of the Bilateralia — *i.e.* of all forms above the Cœlenterata. It is generally agreed that the bilateral type of structure arose by the modification of a radial type, but as regards the mode of transition two totally different views are maintained. Under the older view, still maintained by some morphologists, the long (or principal) axis of the radiate body — *e.g.* of a *Hydra* or a sea-anemone — corresponds to the long or antero-posterior axis of the bilateral body; and hence the oral face corresponds to the anterior end, and the aboral face to the posterior. The mouth must therefore correspond in the two cases, and the anus of Bilateralia is a new formation. Under the more recent view — which is held by the greater number of morphologists — the long axis of the bilateral body corresponds to one of the *transverse* axes of the radiate body, and the oral face of the latter is represented by the ventral aspect of the former.¹ The justification of this view — which to me appears the only possible one — lies in the facts of embryological development. The gastrula stage of development is all but universally regarded as being, in a broad sense, the embryonic representative of the radial, two-layered, ancestral type. The blastopore (or gastrula mouth) represents the ancestral mouth (or protostome). Hence the mode of transition from the radial gastrula to the bilateral adult should give us decisive evidence in regard to the ancestral transition. Now, it has been shown in the clearest manner that, in the great majority of cases, at any rate, the blastopore occupies

¹ This applies, of course, to the bilateral invertebrates only. The vertebrates are left out of consideration, as having, in all probability, arisen from forms to which the statement would equally apply.

taken to mean that bilateral animals have arisen from radial forms by elongation in one of the transverse axes of the latter, the oral face becoming the ventral aspect, and the aboral face the dorsal. The mouth, meanwhile, shifted its position so as to lie near the anterior extremity of the new long axis, and the lateral portions, growing together more or less completely along the region formerly occupied by the mouth, gave rise to the process of concrescence in the ontogeny. What, then, was the origin of the anus of bilateral forms? Here again the answer of embryology appears to be nearly or quite conclusive. The blastopore gives rise sometimes to the mouth, sometimes to the anus, sometimes to both. The only possible interpretation of these facts would seem to be that the blastopore originally gave rise to both mouth and anus, the case of *Peripatus* being an interesting and apparently isolated remnant of the ancestral mode of development, or perhaps a reversion to it. Under any other view, as has often been pointed out, we should be reduced to the absurdity of regarding the mouth of one animal as homologous with the anus of another, perhaps closely related, form; or we should be involved in other difficulties, equally great. The original mode of closure of the blastopore has been secondarily modified in the great majority of cases, but the mesoblastic bands and the neural cords still follow the original mode of development, being laid down separately on either side of the region of the blastopore, and growing together along its line of closure.

Let us now turn, in the last place, to the significance of the trochophore. A very little consideration will

veloped, individualized head, which carries within itself a minute, rudimentary trunk—just as in a seed two huge modified leaves, the cotyledons, carry between them the minute germ of the stem, root, and foliage-leaves. If the cells in question can be shown to be always present the trochophore is not a diploblastic organism, but a triploblastic one, and Kleinenberg's comparison of the trochophore to a medusa falls to the ground. Kleinenberg asserts that the trochophore consists at first of the ectoblast and entoblast alone, the mesoblast being a later formation. This conclusion is based upon the study of *Lopadorhynchus*, in which the mesoblast is apparently not present at the start but is afterwards split off from the ventral ectoblast. This result has always seemed a very puzzling one, which could not be harmonized with what is known of the mesoblast formation in the earthworm, the leeches, and many other forms. I have recently been able, however, to examine the development of an annelid (*Nereis*) which I believe solves the puzzle and shows how *Lopadorhynchus* is connected with the other forms. The early trochophore seems to be diploblastic, as in *Lopadorhynchus*—i.e. to consist of ectoblast and entoblast only, without any trace of mesoblast. In later stages mesoblast arises from the anterior ventral portion of major outer layer ("ventral plate"). A study of the early neurulation of development however—which Kleinenberg did not succeed in following—shows that the cells of the ventral plate are differentiated from the remaining outer line of cells almost from the beginning of development,

Let us see without the use of reagents can be easily distinguished from the remaining outer layer cells in the fully formed "diploblastic" trochophore. *These cells have*

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hypothesis, and this solution is one that many embryologists would be unwilling to accept. I think the great majority of morphologists will agree that no satisfactory explanation of metamerism has yet been given; and the problem of apical growth is still farther from a solution. Concretescence stands on a very different footing, since clear and definite causes for it can be assigned; yet even here a complete solution of the problem will only be possible when comparative embryology has advanced far beyond its present standpoint. As regards the trochophore, opinion is still divided; and I am giving only a personal view in stating that the accumulating evidence seems to favor, in the main, the view that it is a secondary larval form, which gives no clue to the ancestry of the segmented animals. To those whose interest in science lies in the consideration of its positive results only, the outcome of this discussion will doubtless seem rather unsatisfactory; and it must be admitted that in some respects the fundamental problems of annelid and vertebrate morphology seem to be as far from a solution as in the time of von Baer. To the investigator, however, it is the unsolved problems that call forth the deepest interest. It is the very vagueness and uncertainty of the subject that impress upon us how much remains to be done in the embryology of annelids, and arouse the interest with which we look forward to the results of future investigation in this field of study. That the problems of metamerism and apical growth will ultimately be solved, there can be little doubt; but the present need is for new facts, not for new theories. When the facts are forthcoming, the theories will take care of themselves.

form (Haeckel, Lankester, Balfour, Bütschli, and Metchnikoff).

Von Ihering suggests¹ the possibility of the transformation of a multinucleate protozoan into a metazoan by the segregation of the protoplasm around the various nuclei, whereby the organism becomes multicellular, the original Infusorian mouth becoming the mouth of the multicellular animal, and the contractile vacuole its excretory system. This theory, however, has not been received with any degree of favor, inasmuch as it lacks confirmation from the developmental phenomena of the Metazoa, the cases in which the segmentation results in a syncytium (Crustacea, Insecta) being evidently a secondary modification due to the accumulation of food-yolk. There can be little doubt but that the segmentation of the ovum and the resulting formation of a morula or blastula are most readily comparable to the development of a colonial protozoan, and the theories based upon this idea are more worthy of consideration than that advanced by von Ihering.

The first of these theories in point of time, and the one which has had the greatest influence upon embryological investigation, is Haeckel's well-known *Gastræa* theory. This made its appearance in 1872, and was the outcome of the researches embodied in the classic "*Monograph of the Calcareous Sponges.*" The simplicity of structure of the lowest calcareous sponges, and their apparent similarity to the gastrula of the higher forms, a similarity all the greater to the mind of Haeckel on account of his erroneous conception of the structure of

¹ H. von Ihering. *Vergl. Anatomie des Nervensystems und Phylogenie der Mollusken.* Leipzig. 1877.

ovum is a cytode, the next stage in the process of evolution according to Haeckel's scheme, and that it returns for a few minutes to a lower grade of organization simply to indicate its ancestry is certainly an idea at variance with all morphological principles. Thanks, however, to our more perfect technique, we now know that the original nucleus of the ovum does not disappear but is the direct ancestor of the nuclei of all the cells composing the organism resulting by development, and there is therefore no Monerula stage in the developing ovum.

The next stage of evolution was the formation of a nucleus, by which the Monerula was converted into a cell or cytode, the ancestral form being a *Cytula* equivalent to the existing *Amæba*. Following this came the *Morula*, represented ontogenetically by the morula stage which occurs in the development of certain forms, and during which the embryo consists of an undifferentiated solid mass of cells. That this stage can be considered primitive, and the early appearance of a segmentation cavity which is found in so many forms a secondary condition seems however very doubtful. The evidence at our disposal points the other way. No living representative of the morula stage is known, and to fill this gap Haeckel proposes an hypothetical ancestor, the *Synamæbium*.

The fourth stage is the *blastula*, a hollow sphere produced by the usually contiguous cells of the morula secreting a fluid, which, passing to the interior, forces the cells to the periphery. The hypothetical ancestor corresponding to this ontogenetic stage is termed the *Planæa*.

The fifth stage is the *gastrula*, formed from the

note of which is the formation of the endoderm primarily by delamination, invagination being thus a secondarily acquired phenomenon. Thus Lankester's views stand in direct contrast to those of Haeckel.

Like Haeckel, Lankester attempts¹ to give the different historical phases recapitulated in ontogenetic development. He starts with the ovum, the *Monoplast*, corresponding to Haeckel's second stage, the *Cytula*. This is succeeded by the *Polyplast*, equivalent to Haeckel's third and fourth stages, for Lankester recognizes two different forms of *Polyplast*, — one in which it is solid, the *Morula*, and another in which it is hollow, the *blastula*, derived from the *morula* in the manner indicated by Haeckel. Up to this point the only difference between the two authors is the omission by Lankester of the *Monerula* stage. To the *Polyplast* succeeds the diploblastic *Planula*, for which Salensky's more convenient term *Diblastula* may be employed. This is a two-layered vesicle without a mouth, the inner layer of cells (endoderm) having been formed by delamination. The cavity of the *blastula* (*blastocæl*, Huxley) has now become the digestive cavity, or archenteron, the cells lining it having gradually acquired a digestive function while they still formed the inner ends of the *blastula* cells, the acquisition of the function leading to their differentiation from the non-digestive or ectodermic portion.

Delamination is, however, a relatively unusual occurrence, invagination replacing it in a large number of cases. How can its occurrence be explained on the basis of the *Planula* theory? The changes which led to the

¹ E. Ray Lankester. Notes on Embryology and Classification of the Animal Kingdom, etc. *Quart. Journ. Micr. Sci.* vol. xvii. 1877.

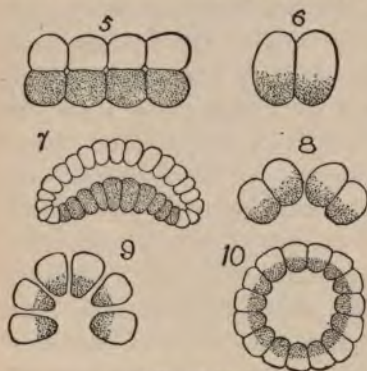
delaminating blastula, inasmuch as it does not become the archenteron on the formation of the endoderm, but is obliterated by the invagination. It is necessary then to distinguish between the delaminating blastula and the invaginating "pseudo-blastula," and between the archenteric blastocœl of the former and the "pseudo-blastocœl" of the latter.

The ingenuity of this theory is its strong point, but simplicity can hardly be considered one of its characteristics. It has not met with the general acceptance which greeted its predecessor and rival, nor has it had the same influence on embryological investigation, — a result owing to the fact that no evidence in support of such an origin of the gastrula can be found.

A third theory is due to Balfour, and may be termed the *Amphiblastula* theory.¹ It is founded upon the peculiar blastula of the calcareous sponge *Sycandra*, the cells of which at one pole are columnar and ciliated, while those of the other pole are larger and granular. Balfour thinks it possible to consider this larva as a colony of Protozoa one-half of the individuals of which have been specialized for locomotor and respiratory purposes, while the others are essentially nutritive. In the later stages, however, the ciliated cells become invaginated within the granular ones, a fact which seems at variance with the theory if the granular cells are to be homologized with the endoderm of other forms, but which Balfour explains in the following manner. On the settling down and fixation of the sponge embryo the ciliated cells, being partly locomotor in function, become, to a

¹ F. M. Balfour. A Treatise on Comparative Embryology, vol. i. London. 1880.

the cells of the two layers, but later one layer might specialize for nutritive purposes, and the other for locomotor (Fig. 5). From such a condition, by the gradual bending of the plate so that the nutritive layer becomes concave (Fig. 7), a gastrula could readily be pro-



FIGS. 5-10.

duced, and in this connection Bütschli points out that the concavity would be useful to the colony, serving as a trap for food-particles and also allowing a larger number of cells to come into contact with a larger food body.

The blastula which so frequently precedes invagination could be produced from this by the accumulation of fluid between the two layers; and furthermore, delamination may have been brought about by the plate, while still one-layered, becoming concavo-convex (Figs. 6, 8 and 9), and finally a hollow sphere (Fig. 10), the transverse division of the constituent cells then taking place.

Unfortunately for this theory it does not find general support in embryological phenomena, nor any more than the Planula theory does it explain the formation of the blastula in a manner in accordance with the actual facts.

There is a series of phenomena which none of these theories attempt to explain. Many of the authors who have recently contributed to our knowledge of Coelen-

dusæ delamination may produce a hollow diploblastic embryo without the intervention of a solid condition. The formation of a solid morula during segmentation which occurs in such forms as *Hydractinia*, *Clava*, etc., may readily be regarded as a precocious immigration, finding its counterpart among the Sponges in *Chalinula*. (Kellar).

In the Scyphomedusæ some forms such as *Pelagia*, *Cyanea*, and *Chrysaora* have long been considered to have an invaginate gastrula. Regarding *Pelagia* there is no doubt that this is really the case, and Metschnikoff has described the occurrence of invagination in *Nausithoe*. As regards the other forms, however, the observations are not sufficiently complete to render the occurrence of this process certain. Sections are absolutely necessary for a correct determination of the processes which occur, and Goette's observations on *Aurelia* and *Cotylorhiza* show that a structure exactly resembling an invaginate gastrula may be produced from a solid planula formed by migration. My own observations on *Cyanea arctica* demonstrate the occurrence in its development of a solid planula formed apparently by immigration, and it seems probable from Claus' figures that such is also the case in *Chrysaora*.

Among the Anthozoa it is very doubtful if invagination ever occurs. In the majority of forms investigated delamination is the process by which the inner cells are formed, but invagination has been stated by Kowalewsky to occur in *Cerianthus membranaceus* and *Actinia*, sp. (?) In *Metridium marginatum* I have found what renders doubtful the statements of that author, who studied optical sections only. A hollow blastula results

tain of the superficial cells became amœboid and migrated into the interior of the colony just as we find them doing to-day in *Protospongia*, and that, in addition, certain other cells divided transversely, one of the cells so formed passing into the interior, while the more peripheral one retained its position at the surface. . . . While transverse division became predominant in some forms, longitudinal division and consequently the immigration of superficial cells prevailed in others. In this manner from mixed delamination, primary delamination branched off on the one hand, and multipolar immigration on the other."

Is it necessary though to assume that this "mixed delamination," *i.e.* a mixture of delamination and immigration, was characteristic of the ancestral flagellate colony? May we not claim that immigration is the more primitive method, and that delamination has been secondarily acquired after the group Metazoa had been well established? There is evidence in the colonial Protozoa in favor of such a view; as, for instance, in *Protospongia* in which cells, originally seated superficially in the jelly in which the individuals of the colony are imbedded, pass to the centre, losing their flagella and collars, and becoming, according to Saville Kent, reproductive. *Volvox* again, when mature, is a hollow sphere with reproductive cells lying freely in the central cavity; these cells were originally at the surface, but, losing their flagella, they migrated to the centre. The same process too is found in the sponges in *Ascetta*, and Metschnikoff has demonstrated its prevalence over delamination in the metagenetic Hydromedusæ.

If this idea be accepted, however, how can delamina-

Invagination can readily be deduced from immigration. Metschnikoff points out that immigration may take place irregularly over the entire surface of the blastula (multipolar immigration), or may be confined to the posterior extremity, especially in free-swimming blastulas (unipolar immigration). It is interesting to note, in this connection, that according to recent observers there is a tendency towards unipolar immigration in the case of the sexual cells of *Volvox*. From the polar immigration Metschnikoff deduces invagination. In the Hydroid *Laodice* a few cells at the posterior extremity of the blastula are clearer than the rest and gradually migrate into the interior. If these cells should migrate *en masse*, instead of individually, we should have such an invagination as occurs in *Nausithoe*, the alteration of the manner of migration being an abbreviation of the original process.

The simplicity of this explanation recommends it, and it serves to clear up the sporadic appearance of invaginate gastrulæ in the Sponges and Scyphomedusæ. But the occurrence of these gastrulæ suggests the question, when once the invaginate gastrula has been established, does invagination continue to be the mode for endoderm formation, other processes, such as epibole, being derived from it? A negative answer to this question involves the assertion that the invaginate gastrula may have been developed several times independently. Is this impossible?

We have invagination occurring in the Sponges and in the Discomedusæ. The gastrula of *Sycandra* cannot be regarded as having been the cænogenetic ancestor of the gastrula of *Oscarella*, and neither of these that of

itself that the epibolic gastrulation which is found in these two somewhat widely separated groups can hardly have arisen independently, and that its occurrence is due to its having been the mode of gastrulation in the ancestors of both groups. It is also to be found in members of other groups, such as the Annelida, having been first described by Kowalewsky in *Euaxes*, and it occurs more or less typically in many Polychætous forms. I endeavored to express this idea in the following statement: "The modes of segmentation of the Platyhelminths, Annelida, Mollusca, and Molluscoidea, can be referred to a common type, indicating that the ovum (so to speak) in all these groups has been derived from an ovum possessing a considerable amount of nutritive yolk aggregated more or less completely at one pole." A necessary corollary of such a proposition I also stated as follows: "The regular and equal segmentation which occurs in certain forms in several of these groups cannot be considered the original mode, but has been secondarily brought about by the loss of a food-yolk originally present."

It would not be suitable in a lecture of this kind to review the various accounts of segmentation in these groups, but I would simply point out that if this idea is correct it follows that epibolic gastrulation is more primitive than embolic, the latter having been derived from the former by the loss of food-yolk. Can epibole have arisen from immigration? It can be regarded as a process of migration, the migrating cells being specialized very rarely in the development, having stored up within them a large amount of yolk. The protoplasm separates more or less from the large yolk spherules,

A large section of the blastula wall migrates at once, and it takes some time for the opening so made to be obliterated. This obliteration is the "closure of the blastopore." The stage succeeding this is the Parenchymella stage, though owing to cænogenetic modifications and acceleration in the development of organs, the comparison is not perfect, but the embryo consists of an ectodermal layer with a central mass of cells in which differentiation has commenced. The blastopore or prostoma of the Turbellarians and Gasteropods has no exact counterpart in the Cnidaria; it is the result of the method of enclosure of the central cells. It is the later formed mouth, or mouth and anus, which corresponds to the Cœlenterate mouth, and just as the mouth forms in the Cœlenterates at the pole where the immigration occurred, so in higher forms the mouth, or mouth and anus, appears at the pole of the embryo formerly occupied by the larger yolk bearing cells. In embolic gastrulas, where the invaginated inner layer of cells forms a hollow sack, the archenteron, it may be to the advantage of the embryo, little or no food-yolk being present, for the blastopore to persist, complete closure never taking place, a portion of the blastopore being converted into the mouth or anus as the case may be. Even in the Echinodermata, however, in which as a rule the blastopore persists as the anus, a complete closure of it occurs in the Crinoids.

This view of the relation of the blastopore to the mouth and anus does not necessarily conflict with the theory first advanced by Bütschli, and later supported by Adam Sedgwick and E. B. Wilson, to the effect that the mouth and anus of the higher Metazoa correspond to

less similar cells, that those individuals which were laden with food matter should not remain at the periphery, but should pass to the centre, not only to equalize the weight of the various parts of the colony, and to allow the more active cells free action at the periphery, but also to permit these food-laden cells to carry on their assimilative functions without disturbance from external conditions.

"For a long time the individuals of any colony probably differed only quantitatively; the locomotor cells attracted food particles by the movement of their flagella and also absorbed some of the smaller particles, just as the ectoderm cells in some Cœlenterates of to-day occasionally ingest food-matter. The inner amoeboid cells, however, were on the other hand capable of swallowing larger food particles. Probably when so engaged the amoeboid cells approached the periphery, and gained possession of food particles lying on the surface of the colony by means of the numerous pores between the cells of the superficial layer. . . . Gradually the differentiation in this direction progressed; the locomotor cells lost more and more their food-ingesting function, which concentrated itself in the amoeboid phagocytes; the occasional fine pores between the locomotor cells enlarged and became openings similar to those so numerous on the surface of a sponge. . . . With the increased activity of the Metazoa, now provided with two primitive organs, there must also have been an increased necessity for food, and larger plant and animal organisms must have served as prey. To make this possible one or more larger openings arose, which led to the formation of a mouth."

organism with a mouth, endoderm, and mesogloea, and also gives a clue to the causes which have brought about the change. The central cells of the hollow planula become transformed into the mesogloea and endoderm, the number of cells contributing to the latter layer being relatively few. The mesogloéal cells have various functions, some producing spicules or horny fibres in some sponges, but a large number remain indifferent or unspecialized to a greater or less extent, some becoming reproductive.

We find too that the endoderm becomes differentiated from the central mass long before the cavity it encloses has any communication with the exterior, and cannot very efficiently function as a nutritive layer since it is separated from the outside world not only by the thin ectoderm, but also by the thick mesogloea. It is necessary that respiration should be carried on throughout the entire mass of the sponge. While it is small this is readily effected through the ectoderm, but as it grows, the mass increases so much more rapidly than the surface, that this simple method no longer suffices. Cavities appear here and there in the mesogloéal mass, and later communicate with one another, the cells lining them becoming ciliated to produce a more rapid circulation of the water. A large central space into which the various cavities finally open makes its appearance, and last of all this space breaks through to the exterior, forming the *Osculum*. The water which at first reached the cavities by filtration through the tissues, later on has ingress by pores, and the complicated canal system of the sponge is established.

In its first inception, then, the canal system and the

Other cases might be given having a more or less direct bearing on this question, but the time at my disposal prevents a fuller treatment of the subject. I would like, however, to refer to one case, namely, Grobben's account of the development of the Phyllopod *Moina*. We have in this form three distinct invaginations: (1) an invagination of certain cells to form the endodermal midgut; (2) of certain cells to form the general mesoderm; and (3) of four cells to form the reproductive organs. Only one of these, however, the first, can be considered a true invagination; the others are more correctly immigrations. The entire process can, I think, be referred to the formation of a parenchymella in which there has been a precocious segregation of certain important organs. The germ plasma has been early segregated into a certain spherule of the developing ovum and accordingly immigrates independently of the general mesoderm cells, whose perfect segregation, like that of the endoderm, is postponed to a slightly later period, these two last-named structures likewise immigrating independently.

There are some cases, however, which seem to throw serious obstacles in the way of the view as to the origin of the endoderm and the reproductive elements which I have advanced. In the Hydrozoa and Ctenophora, the reproductive cells have been shown by Weismann, and the Hertwigs especially, to be derived from the ectoderm. The latter authors endeavored, on this account, to associate the Hydrozoa and Ctenophores together as distinct from the Scyphozoa, in which the reproductive cells have an endodermal origin. Other structural peculiarities, such as the presence of an ectodermal stomato-

modify it in its essential points in the least. They are merely suggestions which have developed during the consideration of the application of the theory, and must be regarded simply in that light. For a complete exposition of them much more detailed description, unsuitable for an occasion of this kind, would be necessary, and I present them here merely in the hope that they may incite to more thorough and perfect acquaintance with the problems connected with the early development of invertebrated animals, and the bearings of the ontogenetic phenomena on the question of the origin of the Metazoa and of their organs. I cannot do better than quote in conclusion from Metschnikoff, "*Es musste gerade im Bereiche der niederen Metazoen ein fester Boden für das Verständnis der primitiven Organe gewonnen werden.*"

generative glands, and being thus transmitted to the young, seemed too cumbersome and complex for general acceptance.

Quite recently Professor Weismann of Freiburg has advanced a theory of Heredity which seems by far the best hitherto offered. This theory is the culmination of a train of thought which he has put forward in essays from time to time during the last few years. These show the gradual growth and development of the theory in the mind of the author, and though some of the facts from which he argues may be open to dispute, yet the ideas which he suggests are so interesting that they are entitled to consideration, even though subordinate to the main plan of his theory.

In one of his earlier essays he points out that the manner of reproduction among the Protozoa is such that death does not normally occur in this group, for the animal reproduces by merely dividing itself into halves. Thus an adult animal ceases to exist as such, by becoming two animals instead of one. It does not die during this process, for there is no corpse, but the whole animal as such has completely disappeared, and in its place we find two individuals so similar that it is impossible to regard them as parent and offspring. Indeed, they cannot be parent and offspring, for they are of the same generation, — it is more natural to call them twins. They are both young animals, for they increase in size, and when adult each of them ceases to exist by dividing itself into two new young ones, and so on indefinitely.

Hence it would appear that the life-history of such an animal may be divided into two periods, — youth and

protoplasm which will cause it to fall short of its cycle, and to physiologically decline. He does not mean that such unicellular forms cannot be starved to death, crushed out of existence, devoured, or killed by disease. These are rather accidental than natural deaths. He claims only that since life has existed in these forms, it has passed unbroken from one generation to another down to to-day. The material of which the individual is made may change, but in all cases it is animated by the same life.

Now no one doubts that the Metazoa have at some time in the remote past been evolved from such potentially immortal Protozoa. But the life of all of the Metazoa may be divided into *three* periods, — youth, adult life, and old age, during which latter there is clearly a physiological decline in vigor, which is terminated normally by death.

Old age and death then would appear to be something which have been acquired with the development of the Metazoa from the Protozoa.

Exactly for what purpose, and how, death has been instituted are questions which Weismann endeavors to answer.

But first let us compare the life-history of a Metazoön with that of a Protozoön, and see whether there is anything in the Metazoa which is comparable to Protozoa immortality. All Metazoa start their individual lives from an ovum, which is a single cell, and may well be compared to a Protozoön. After fertilization this cell or ovum divides into two, then into four, then into eight cells, and so on, thus giving rise to a very large number of cells which, as development progresses,

which has been acquired through natural selection during the evolution of the Metazoa from the Protozoa. Whether this conclusion is just is to a certain extent a side-issue to the theory of the continuity of germ-plasm, and further on the matter will be more fully discussed.

Among the Protozoa it is very evident that the young must resemble the forms from which they spring, for they are a part of the same stuff. Furthermore, if during life an individual becomes changed by its environment, this change must become an hereditary trait.

Now we may assume that the Protozoa may be affected by the physical conditions under which they live just as much as are the Metazoa. It is a well-known fact that the bodies of the higher forms may be changed by food and exercise. The muscles of a blacksmith or a sailor are stronger than those of a dude.

A *Paramæcium* which lives in a strong-flowing stream would be apt to acquire stronger cilia than one living in a stagnant pool. The young which spring from a *Paramæcium* with strong cilia must inherit this character. Indeed, the cilia of the young are the identical cilia which by constant use have been lengthened and strengthened. In every case of reproduction by fission, the whole body of the parent continues its existence in the younger generation. If the parent is strong and vigorous, the young are so likewise; if the parent is decrepit and feeble, the young must likewise be decrepit and feeble. Hence all modifications which any unicellular organism may acquire must be transmitted to its young.

young are not affected. Mutilation, among savages, of the nose, face, and ears has been carried on for generations, yet no traveller has reported that either the mutilations or the scars are inherited. All these facts should be borne in mind when it is claimed, as it still is by many, that acquired characters may be and are inherited. Weismann admits that the long-continued effect of climate and food may to some extent act on the germ-cell; but the idea that species can have originated through the inheritance of the peculiarities acquired by their ancestors, is contrary to his theory.

Now the young of the Metazoa inherit the main characters of their parents, for the same reason that the young Protozoön resembles the form from which it springs, — they are made of the same stuff. Germ-cells and body-cells arise from the same germ-cell. During the development of the individual the immortal portion of the germ-cell is set aside to form the next generation. The characters which the body of the individual may acquire during life must be very fundamental to affect these germs. A young Metazoön is a part of its parent, because the stuff of which it is made is a part of the germ-cell from which its parent was made. It may also resemble a grandparent or a great-grandparent, for its parent sprang from a part of the same germ cell which built its grandparent. Its great-grandparent was in turn a part of its great-great-grandparent. Thus every individual is made up of the same material as its ancestors, in degrees varying with the different generations. In ten generations an individual may have 1024 ancestors, of all of whom the individual itself is a part. If the theory of the continuity

ovum to develop by introducing spermatozoa. A new nucleus was then formed by these, and the ovum developed into a free-swimming larva.

If before sexes were fully established, two germ-cells of different origin were to unite, the embryo would have a dual origin, and hence would differ from both parents. If the variation thus introduced were favorable, survival of the fittest would preserve it. The germ-cells of this form would, of course, inherit the tendency to unite with another germ-cell. In this way natural selection would establish sex, to ensure the combining of two germ-plasms in each individual. Without such combination no variation in the Metazoa could occur. Hence all sexual characters—even to the higher mental attributes—are due in their origin to the necessity of establishing variation. Variation, then, is a consequence of the union of two sexual germ-plasms, and not something inherent in protoplasm.

At first thought it seems strange that variations are not more numerous and marked than they are; that for thousands of years the germ-plasm of every species of animals has undergone so little change that each species still retains all its specific characters. It would seem that if animals are not suited to the environment, they are not modified, but exterminated. Yet when advantageous variation has occurred, and the race has been preserved by natural selection as a different species, this must have been brought about very slowly. It is thus evident that the plasm is very conservative and difficult to change; that the conservative forces far outweigh all tendencies to vary.

Now to return to the question whether death is

perfect eyes, the eyes of the whole race would begin to degenerate. Take another case, such as is offered by birds of prey, which are possessed of exceedingly sharp sight. If some of these birds happened to come into the world with defective eyes, they would starve to death, or at least be less likely to succeed than their brethren which were more fortunate in this respect. Hence sharp sight is maintained by the continued operation of natural selection, which tends to exterminate those with defective sight. But let these birds come to live under conditions in which those with defective sight got along as well as those with keen sight, — say in a dark cave, — and it would seem more than probable that the eyesight would degenerate. Those which varied in the direction of defective eyes would survive as well as the others. Hence they would breed with the keen-sighted ones, and thus gradually the general average would be lowered. Another example must suffice. Short-sightedness is not at all uncommon among civilized races, and is generally believed to be hereditary. Short-sighted men succeed in life as well as those with normal or very keen sight. Neither natural selection nor any other selection compels keen sight. But a short-sighted hawk or antelope, or even a short-sighted Indian, would be placed at so great a disadvantage that short-sightedness would soon be eliminated from the race.

In these last-mentioned forms natural selection compels the eyes to come up to a certain standard, while among civilized men and cave animals there is no such necessity. Natural selection maintains only what is an advantage, and when it neglects an organ, that organ tends to degenerate.

rest of the colony withers up and dies. Hence we find in *Volvox* the first approach to a differentiation into germ and somatic cells.

Since Weismann made this startling assertion, that death is not an attribute of all living organisms, much opposing evidence has been brought forward. Most prominent and recent among his opponents is E. Maupas, of Algiers, who, after extensive study of some of the Infusoria, asserts that degeneration and death occur as normally among the Protozoa as among the Metazoa. Before entering on his experiments, Maupas first determined very carefully the habits of the different species which he chose for study. He found out the temperature to which they were best adapted, and the kind of food on which they thrive best. Then he took a single individual, and isolated it on a glass slide, on which it could be studied. This slide was kept over a dish of water in a warm, damp chamber in which the air was so thoroughly saturated with moisture that evaporation was reduced to a minimum. During its confinement the animal was fed on its favorite food, and in every particular what seemed to be the most suitable conditions were maintained. He found that at the end of seven days there were no less than 935 Infusoria in his culture. One of these 935 he isolated and kept as he had the first. In four days this single one had increased to 230. One of these was isolated in the same way, and this process of isolating and confining one individual of each brood was continued through a large number of generations. He shows the rapidity of increase to be something almost incredible. Calculations show that in six and a half days a single *Stylonichia*

comes impossible, and death follows. Thus it would appear that the life of these animals is cyclic. During the period of reproduction, which is the adult life of the animal, a sort of physiological decline takes place, and this decline can be repaired only by conjugation.

Now if during these experiments the animals have not been injured or poisoned, it would seem that Maupas had proved that death may occur normally among unicellular forms.

Weismann, however, is not ready to admit this. He claims that conjugation is a necessary condition of the animal's life, just as fertilization is a necessary condition for the survival of an ovum, and if conjugation is denied, the death in consequence is accidental and not natural; further, that the fact that conjugation is necessary does not imply that the protoplasm is not potentially immortal. He seems, however, to overlook the fact that a certain physiological decline has taken place, and that if there is any physiological decline the cycle of life is incomplete; therefore the seeds of death must exist inherent in the life of the animal. It is, then, for the present, impossible to speak of the Infusoria as potentially immortal, and to claim that that portion of the Metazoa which undergoes physiological decline has no equivalent in these forms. Nevertheless, it is too soon to declare that the idea that death is an adaptation is altogether erroneous.

In many well-known unicellular forms, neither a physiological decline nor a process of rejuvenation has been observed. The Bacteria, the Cyanophyceæ, and Yeast increase by budding, spore building, and fission, and

juvenescence by conjugation. In other words, those to which it was an advantage to retain their immortality have retained it, and those which varied in such a manner that immortality could be advantageously replaced by rejuvenescence have, by the action of natural selection, undergone this modification. If this is so, Weismann's error is not in claiming that death was an adaptation, but in asserting that all unicellular forms are immortal.

Still another and earlier opponent of Weismann has urged serious objections to this theory of the origin of death. Professor Charles S. Minot was the first to maintain—and many have taken up his suggestion—that Weismann is fundamentally wrong in comparing the life-history of a Metazoön, which is a complex colony of cells, with that of a Protozoön, which is a single cell. Minot urges that an individual Metazoön is comparable to a colony of Protozoa, not to a single cell. If this be so, then the death of a Metazoön (a colony of cells) has its only homologue in the degeneration and death of a culture of Protozoa. The Metazoön colony is the product of a single germ-cell, as is also the whole culture of Infusoria.

This comparison seems safe between the Metazoa and those forms of Protozoa which conjugate, and in which senile degeneration occurs. But how is it when we bring those which do not conjugate under consideration? If this view be correct, then a single Metazoön is equivalent to all of a species of Bacterium which may arise through generations of fission. As far as our knowledge goes, these Bacteria are immortal and their numbers almost infinite. We know, on the other hand, that

years, and each year lays about twenty eggs. Hence a pair of partridges may produce about four hundred eggs in their lifetime. This is at the rate of two thousand in a hundred years. Yet, since the number of partridges in the forest does not increase, three hundred and ninety-eight of these eggs, or young, must be destroyed in twenty years, while but two survive to take the place of their parents. The eggs and young are destroyed by beasts and birds of prey. If these enemies increased very much in number, the partridge would become extinct unless it laid more eggs.

It would appear, then, that the partridge lays just eggs enough to ensure the continuance of its race, and this being accomplished, death removes it. Many species have doubtless become extinct through the insufficiency of their reproductive powers. The number of offspring which, under ordinary conditions, would have ensured perpetuation, has proved insufficient when their enemies increased or the environment became unfavorable. The supply must be equal to the demand.

Now for the eagle. The eagle is one of the most powerful of birds, and builds its nest on such inaccessible cliffs that eggs and young are comparatively safe from marauding animals. Many, however, are destroyed by late frosts and snows. To be on the safe side, let us fix the duration of life of the eagle as sixty years, and of this ten years is spent in immaturity. Hence there are fifty years of its life during which it reproduces. If the eagle lays but two eggs a year, a pair of eagles would produce one hundred during their lifetime. In a hundred years two hundred eggs against

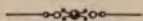
their lifetime, a pair of elephants contribute but ten or a dozen young to the race.

Wallace shows that we are living now in a zoologically impoverished world. Almost all of the largest and strangest forms have recently become extinct: in Europe the great Irish elk, the sabre-toothed tiger, cave-lion, rhinoceros, hippopotamus, and elephant; in North America equally large felines, horses, and tapirs larger than any now living, a llama as large as a camel, mastodons and elephants, besides a large number of huge megatherians; in South America an even greater number of megatherians, huge armadillos, a mastodon, large horses and tapirs, large porcupines, two kinds of antelopes, numerous bears and felines, beside the sabre-toothed tiger.

Remains of all these are found in the recent deposits, and these animals lived till shortly before the northern continents were encased with the ice of the glacial epoch. It is possible that a change of climate, due to the growing cold from the encroaching ice-belt, affected the flora. This would, of course, affect the food supply, and so tend to lessen the reproductive powers, and shorten the lives of the individuals. Lessened reproductive power and shortened lives of the individuals would surely result in the extinction of the race, and in this way the destruction of these forms may be accounted for. The starvation of the individual is therefore synonymous with the starvation of the race.

The main features of Weismann's theory may be summed up as follows: *First*, The continuity of the germ-plasm. *Second*, Variation is due to the different molecular combinations formed in the mixture of the

SIXTH LECTURE.



EVOLUTION AND HEREDITY.

By HENRY FAIRFIELD OSBORN.

I WANT especially to direct your attention to the relations between our present knowledge of the evolution process and the problem of Heredity. The mere truth of the origin and succession of life by evolution may now be demonstrated in every branch of Biology, the arguments from palæontology, embryology, and morphology being equally convincing, but the theory of the evolution process is inseparably connected with some theory of inheritance. If new individuals were simply repetitions, like coins struck from a species mint, there would, of course, be no evolution possible, and we should perforce return to the Miltonic conception of creation, at the same time greatly reducing the number of difficulties in the heredity problem. While in zoology the repetition phenomena are perhaps the most conspicuous, in palæontology, or, in other words, in the succession of life in time, the variation phenomena are more striking, and we come to realize that the how, why, and when of the variations give zest to the study of the fossil series and furnish the crucial test for any heredity hypothesis.

Second, it must account for the non-repetitive phenomena, or the appearance of new characters, to the importance of which Darwin first directed our attention. It is clear that anthropology, zoology, botany, and palæontology give an ample field for the above. Thirdly, there are the physical transmission phenomena, the peculiar field of the embryologist. We may approach heredity through either of these channels, but the test must be by the data afforded by them all.

Thus we find Lamarck, Darwin, Galton, Spencer, Brooks and others coming to the problem chiefly from the study of living adults in past and present time, while Weismann has come to it from the side of embryogenesis. There are great difficulties in the embryological problem; we have to do with particles of protoplasm of minute size, largely composed of water, yet suspending invisible molecules which we must suppose are the actual vehicles of inheritance, for, under the ordinary conditions of nutrition, they will repeat chapter after chapter in the history of the race, and finally take the form of the adult — they are indeed microcosms. We have to consider the part played by the male and female element. And the relation of these specks of protoplasm to the life history of the individual.

Democritus, who offered the first hypothesis, supposed that the sperm was secreted from all parts of the body of both sexes at the time of impregnation animated by a bodily force, like parts producing like. When Darwin proposed his provisional hypothesis of pangenesis he embodied in it a somewhat analogous conception, but he was aided by the well advanced stage of embryological and physiological science. The older views of

and ancestral traits, and does not accord with the facts of the early appearance and isolation of apparently complete germ cells. Moreover Galton's well known experiment of the transfusion of the blood of eighteen silver-gray rabbits with that of other varieties showed that the gemmules, if existent, do not circulate in the blood, for this transfusion of blood was not accompanied by the slightest interchange of characteristics.

Passing by Haeckel's suggestion of *Perigenesis*, which invests the molecules of organized matter with some of the lower faculties of mind,¹ let us look at Brooks's ingenious attempt to modify Darwin's hypothesis. His postulates were the actual existence of the gemmules, but not quite as conceived of by Darwin, for there is a fundamental difference between the male and female elements of reproduction. The ovum is conservative, reproducing cells like itself and a storehouse of hereditary tendencies, giving rise directly to new ova, while the spermatozoan is the progressive element, the repository of the gemmules. Nor are the gemmules thrown off at random by all the cells of the male body, but especially by those which are disturbed in their conditions by a change in environment. Variability, therefore, is most rapid when external conditions are disturbed, and it springs from the union of the ovum and spermatozoan. This system is open to most of the objections which can be raised against the original of Darwin, but is moreover opposed by the rapidly accumulating evidence for the essential similarity of the ovum and spermatozoan.

¹ See Brooks's *Heredity*, p. 37. "Unconscious memory is the most important characteristic of organized matter. Heredity is the memory of the plastidules; variability, their power of perception."

of Weismann's views are, that the nucleus of the germ cell is the sole bearer of the hereditary tendencies ; that the expulsion of each of the two polar bodies of the ovum has a distinct meaning, the first expelling the ovogenetic nucleoplasm, the second reducing the ancestral germ plasm by one half, and thus rendering the nucleus ready for the accession of the germ plasm of the spermatozoan which has previously been correspondingly reduced. While these subsidiary hypotheses, if correct, would strengthen Weismann's position, I do not see that his theory is dependent upon them.

Now look at his main propositions, first, as against Brooks, there is no fundamental distinction between male and female germ cells ; second, as against Darwin and Lamarck, the early separation and isolation of the germ plasm from the somatoplasm, renders it highly improbable that acquired characters can be inherited, for the changes in the body can exert no definite influences upon the germ cells. It is at once evident that this theory explains admirably the repetition-phenomena, and is strong upon the embryological side. Before criticising it from the non-repetitive or evolution standpoint let us examine the views of Galton.

It is certainly very remarkable that there are so many points of agreement between Weismann and Galton, when we consider their diverse fields of research. Galton was the pioneer, and the fact that Weismann independently reached similar conclusions from entirely different data, affords a strong presumption in favor of their common grounds of opinion — that the physical vehicle of heredity is continuous and feebly or not at all influenced by changes in the individual which conveys it. Some

of characteristics which have the firmest hold upon the race ; as illustrated by a polygonal block with unequal sides : the chances are that the block will fall upon its longest side, yet it may fall upon its shortest side and represent a new type, which, nevertheless, possesses some small stability of its own. Against such stability, however, works the *law of regression*, viz. that upon the whole the stature of children will be more mediocre than that of their parents ; that the more exceptional an individual is, the greater are the chances that his offspring will be unlike him, *i.e.* nearer to the race type. Nearness of kinship must therefore be computed in degrees of regression. 3. In the life history of the individual the influences of nature, or inherited constitution, greatly preponderate over those of nurture, or environment and education. It has been generally held that the study of man affords the most striking examples of the law of inheritance of acquired characters. Yet Galton says, in doubtful terms, that such inheritance should be looked for not in the first but in the second and third generations ; that acquired faculties, if at all, are transmitted with dilution ; that the actual evidence for such transmission is not very conclusive.

It appears to me that if Weismann's system had been especially built up *a posteriori* for Galton's anthropological laws it could not have been better adjusted, but since he makes no allusion to Galton's work we know this was not the case. The balance between variation and stability, the element of certainty and of chance in the mingling of heritages, the reduction of parental and ancestral characteristics are all explainable by Weismann's views of physical transmission. Upon

be quoted in the affirmative, while Wallace, Weismann, Lankester, and the majority of the younger English biologists take the negative. Darwin's later views in this matter are most clearly stated in his correspondence with Moritz Wagner: "In my opinion the greatest error which I have committed has been not allowing sufficient weight to the direct action of the environment, *i.e.* food, climate, etc., independently of natural selection." I quote this because Lankester has tried to show in a letter to *Nature* that Darwin never adopted the views of Lamarck.

The general drift of my own views is that upon the side of evolution, or non-repetition in inheritance, the Lamarckians have much the best of it; while upon the side of repetition and of embryology, their opponents are strongest. It has been said, "Heaven deliver us from our friends," and I must confess that, upon carefully analyzing the arguments of some of the neo-Lamarckians, I find almost as much against as for the principle they are advocating. The palæontological evidence appears to be the least vulnerable. For example, the evolution of the horse's foot seems to afford conclusive proof of the inherited effects of use and disuse; yet when we consider the enormous period of time which the reduction of the second and fourth digits has required since the lower Miocene period, when they became absolutely useless, the force of the argument is somewhat invalidated. Again, in the teeth, the evidence for kinetogenesis is not without exceptions. We require more accurate observation and more logical reasoning, especially directed to the facts of transformation in their bearing upon inheritance.

SEVENTH LECTURE.



THE RELATIONSHIPS OF THE SEA-SPIDERS.

By T. H. MORGAN.

AMONGST the Hydroids and sea-weeds on the piles of the wharf of the Fish Commission, living below the tides, and clinging tenaciously by means of the long jointed legs to the surrounding stems, are to be found abundantly small whitish spider-like creatures. And if the sea-weeds, etc., dredged in the "Hole" be examined, a similar but larger animal may be found.¹ The group to which these belong is known technically as the Pycnogonida, or, as Professor Dohrn of Naples has proposed to call them, Pantopoda. Fortunately we have a good enough English equivalent for the terms — Sea-Spiders.

It may not be out of place to say here a few words about the structure of the adults of these sea-spiders, as the group is a small, isolated one, and only short accounts are given in the ordinary text-books. The accompanying figure (1) may aid us in understanding some of the principal structures of the group.

¹ *Phoxichilium maxillare*.

appendages following the palps is situated more ventrally than either of the other two, and hangs down from the ventral side of the animal. These are the ovigerous legs. These anterior three pairs of appendages are followed by four pairs of walking-legs. The first pair of walking-legs is attached to what we may call the first body segment. To the same segment are attached the proboscis in the anterior middle line, the pair of mandibles, the palps, and the ovigerous legs. In the middle of the dorsal surface of the same segment lie the four small simple eyes.

The second pair of walking-legs (the fifth pair of appendages) is attached to the second body segment, the third pair of walking-legs to the third body segment, and the fourth pair to the fourth body segment.

The body of the animal ends posteriorly in a small process pointing upwards and backwards, which carries the anal opening at its distal end, and is known as the abdomen or rudimentary abdomen.

Turning now to the internal structure, we find a brain—dorsal to the œsophagus—followed by a ventral chain of five pairs of ganglia for the middle region of the body and a pair of small ganglia, continuous with those of the trunk, within the abdomen. The first pair of appendages is innervated from the brain; the palps and ovigerous legs from the first pair of ventral ganglia. This first pair of ganglia is in reality the partially as the first and second pairs. Each of the four pairs accounts a legs has a pair of ganglia in its segment, accompanying it with nerves; and there is, as I have some of the 1 of ganglia in the abdomen. The digestion as a simple straight tube through the

Speaking in general we may say that prior to 1880 the group was placed either amongst the Arachnids (spiders, scorpions, etc.), or else amongst the Crustacea. Recent work has shown Crustacea to be out of the question, I think, but at the same time, the alternative was not believed to be the Arachnids. The group has been independently monographed by Dr. Hoek in a report of the *Challenger* Expedition, and by Professor Dohrn in a volume of the Naples Fauna and Flora. Each of these authors concludes that we are to believe the group to have arisen, independently of other Arthropods (Crustacea, Spiders, Insects), from the Annelids. While their work has been very complete as regards the adult anatomy, and inasmuch as any speculations about the inter-relationships of animals must take into account largely the adult structure, yet there remained unworked another equally valuable source of knowledge; viz. the study of the changes which the animal undergoes in its development from egg to adult. Information from this source must take equal rank at least with that from adult anatomy and histology, and may throw light upon hidden relationships which could not otherwise be obtained; and I wish to give hurriedly a few facts about the embryology of these animals, choosing those which seem to me to bear directly upon the relationship of the Pycnogonids to another group to which a study of the development has led me to believe the sea spiders to be allied.

Without a series of figures to illustrate these stages of development, it will be impossible to do more than merely mention, in the briefest possible way, those points which are to be used in our comparison. Moreover,

hydroids. The first pair are three-jointed, — counting the movable claw of the chelæ, — the second and third appendages on each side are two-jointed. These last



Fig. 2

two appendages represent the palps and ovigerous legs of the adult. The body ends anteriorly in a rounded proboscis. The digestive tract, beginning at the mouth at the distal end of the proboscis, passes through the proboscis as a tube triangular in cross-section and opens out into the wide stomach within the body proper. There is no

posterior opening to the digestive tract, but from the stomach runs forward into the mandibles a pair of diverticulæ. The larva has a brain lying dorsal to the œsophagus, which is connected by two commissures with a pair of ganglia ventral to the digestive tract. There are in all two pairs of these ventral ganglia, the pairs more or less fused together; and behind these, and completely detached from them, is a thickening of ectoderm which indicates the commencement at this place of a third pair. The larva has no heart nor reproductive organs at this stage.

It is needless to follow here the changes which this Pantopod-larva (Dohrn) undergoes as it is metamorphosed into the adult. The body elongates, new appendages appear seriatim, the proctodæum invaginates and puts the digestive tract posteriorly into communication with the outside world, and the second or third pairs of

former case, multipolar delamination; but owing to the large amount of yolk, the delamination begins first in the region of the micromeres, — each cell of which delaminates into an inner and an outer cell, — and this process progresses slowly over the surface of the egg, each cell, both micromere and macromere, delaminating just before it joins the edge of the ever-widening blastoderm. The outer cells of the blastoderm form a somewhat flattened columnar layer, under which lie the nuclei and protoplasm of the inner cells. To the inner cells would belong properly all of the yolk of the pyramidal cells; but as a matter of fact, all traces of cell-outlines are completely lost in the yolk at this time, so that the blastoderm, with its two layers, lies at the surface of a yolk-mass. Soon after this there can be seen at the surface of the embryo a round opaque spot, which I shall call the primitive cumulus. The ectoderm is thickened in this region, and in the centre of the thickening lies the triangular invagination of the stomodæum, and around the latter appear the first traces of the mesoblast.

There next appear at the surface of the embryo other opaque areas, which are the beginnings of the brain, the ventral ganglia, and four pairs of appendages; — viz. the first, fourth, fifth, and sixth. The embryo still retains its spherical shape.

The next stage is shown in ventral view by Fig. 3. By reference to the figure the more important structures can be seen. The proboscis projects forward; on each side of this are the mandibles. On each side of the ventral median line lie five pairs of appendages, and to the sides of the last three are three pairs of walking-

opaque area on the surface — the primitive cumulus; beneath this the first traces of the mesoderm are found, and further, this is the point where the stomodæum soon invaginates. We have seen an exactly similar series of changes in the embryos of the Pycnogonids. We also find body cavities lying at the bases of the legs of the embryo spider, in an exactly similar position to those which we have seen in the sea-spiders. The digestive pouches found in both the adult and in the embryos of the Pycnogonids, which contain yolk in the young, furnish us with another point of comparison with the Arachnids. In the latter, we have these for a time in the developing young; and, moreover, in the false-scorpion they contain yolk from the mesenteron.

Lastly, I must call attention to the structure, innervation, and origin of the first pair of appendages. These are chelate, as in many Arachnids, and the free movable joint of the claw moves outwards and downwards as in the Arachnids generally (and not upwards and outwards as do the chelæ of the Crustacea). Again, these appendages are innervated in the sea-spiders from the brain, and finally in the embryo the appendages are seen to arise at the sides of the stomodæum, and subsequently move forward and dorsal to it. In both of these last characteristics we can compare the two groups directly together.

So much for the embryology: I leave these comparisons to speak for themselves.

And now let us turn to the adult structures of the two groups under comparison.

I do not believe any general definition of the group of Arthropods can be made, which, if based on funda-

abdominal appendage, so that the difficulties arising from the existence of similar openings in the Pycnogonid, on most of the appendages, is partially at least overcome. I have also examined the structure of the adult eyes of the Pycnogonid, which seem to furnish, perhaps, an explanation to the early inversion of the eyes of the Scorpion and other Arachnids.

Let us turn finally to an examination of the appendages of the Pycnogonids, where we meet with a stumbling-block in the way of our acceptance of the relationship of the sea-spider and Arachnid.

If we arrange in two series the appendages of the two groups, beginning with the first pair in each, we get the following table:—

<i>Pycnogonid.</i>				<i>Spider, Scorpion, etc.</i>			
Mandibles	.	.	1st pair	.	Chelicerae.		
Palps	.	.	2d "	.	Chelæ.		
Ovigerous legs	.	.	3d "	.	1st walking-legs.		
1st walking-legs	.	.	4th "	.	2d	"	"
2d " "	.	.	5th "	.	3d	"	"
3d " "	.	.	6th "	.	4th	"	"
4th " "	.	.	7th "	.	.	.	.

In the Pycnogonids there are seen to be seven pairs of appendages, while the spider, etc., have only six pairs in all. There are four of these pairs used by each as walking-legs, and in the Pycnogonids three pairs lie in front of these, and two such pairs in the spiders.

We may get out of this difficulty of numbers in either of two ways. In the first place, we may assume that the four pairs of walking-legs are homologous in the two groups, and at first sight this seems very plausible.

spiders with the first of the sea-spiders, the third with the second, and the fourth with the third, leaving over the fourth pair of legs of the Pycnogonids as a pair not found in the spiders. If this be true the position to which we are forced is obvious, — that the last segment of the body of the sea-spiders, and its appendages, correspond to the first segment of the abdomen of the spiders. Such a transfer of segments is not uncommon amongst Arthropods, and there is nothing unusual in such a process. It here carries with it, however, the assumption that the fusion must have taken place at a time when the abdomen still bore appendages serially homologous with those of the thorax. We may imagine, if we like, that this took place at a time when the third pair of appendages appeared and began to carry the eggs, so that the body, by utilizing the first legs as egg-carriers, retained a pair of the abdominal legs for purposes of locomotion.

I must confess, however, that although this last view seems far the more probable, in the present state of our knowledge, yet the idea is a very attractive one, — that the four pairs of walking-legs are homologous in the two groups, and that therefore the spiders have lost a pair of appendages between the chelæ and the first pair of legs.

I have, in the above comparison, left to one side the Crustacea, nor is there need to say much in regard to their possible relationship to the Pycnogonids. The characteristics which the two groups have in common are only those of Arthropods in general. Other than this there seem to be few homologies, with the possible exception of a six-legged larval form of which I shall

There is another problem, which must arise in any discussion of the affinities of the Pycnogonids, and which may be treated as a corollary to what has gone before. I refer to the presence within the group of a free-living larval form—the Pantopod-larva which we must believe typically to belong to all the species of the order.¹ Was the ancestral form from which the group has arisen similar to this Pantopod-larva, hence its presence as a stage of development to-day; or is it a purely secondary larval form, an interpolated stage, therefore, unimportant from a phylogenetic point of view?

Before attacking the problem directly, let us understand clearly the possible conditions under which such a larval form, or any larval form, may occur within a group of animals. There are at least, two, and perhaps three, such conditions generally recognized. We have first what is known as a primary larval form, by which we mean the young form represents approximately the structure possessed by the ancestor from which the group has arisen. In Fig. 4 this is shown diagrammatically by *A*. The *X* marks the place at which a species *x* expanded into a group, and after the group has been evolved each young form in that group first reaches *X*, and then each in turn develops the peculiar features of its particular family, genus, species.

Again we may find all the animals of a group possessing a common larval form, but which need not necessarily ever have been an ancestor of the group, but may have been *interpolated* quite early in the history of the

¹ Such exceptions, as *Pallene* for instance, show an abbreviation of this development, and at one time they or their ancestors must have had a free-larval form.

a free larval form of its own (whether primary or secondary is immaterial), and as the group arose, through divergence of the adult animals, the larval form was itself affected by the new characters of the adult, and so changed into what I shall speak of as a *transformed larva*, or, to put it differently, we may suppose the newly acquired characters of the adult to be thrown back upon the larval form already present. This is shown by diagram *C*, Fig. 4, when *a* is changed gradually to *ay*, *az*, as the adult *X* changes into *Y* and *Z*.

There may be many modifications of these three conditions I have sketched, but for our present purposes these will suffice.

To restate the problem before us: we wish to find out, if possible, in which of these ways the larval form in the Pycnogonids has been evolved. Professor Dohrn believes, and his theory is the natural outcome of the position he has taken as to the origin of the group of the sea-spiders, that the larva of the Pantopoda is a transformed larva, and therefore the explanation of its appearance within the group to be represented by Fig. 4, *C*. Dr. Hoek, on the other hand, believes the embryo to be a primary larval form, and therefore its presence to be accounted for in some such way as represented by Fig. 4, *A*. Professor Dohrn further believes that the Trochophore of Annelids represents the first larval form which became modified into the Pantopod-larva; while Dr. Hoek believed that the Pantopod-larva of the Sea-spiders, the Trochophore of the Annelids, and the Nauplius of the Crustacea, have each given rise to their respective groups, and to each represent a primary larval form; and moreover, he thought these

nal opening at the posterior end of the body. There is a brain (supra-oesophageal ganglion) dorsal to the oesophagus, connected by commissures with the first pair of ganglia of the ventral chain. An eye lies in the mid-dorsal line over the brain. The first pair of appendages is simple and uniramous and receives its nerves from the brain. The second and third pairs of appendages are each biramous, and the first and second pairs are innervated from ventral ganglia. These I believe are the essential features of the Nauplius. It swims freely

in the water, and lives a perfectly independent life in those forms in which it is best represented.

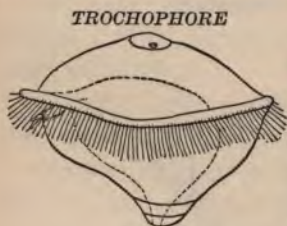


Fig. 6

The Trochophore of the Annelids is likewise a free-swimming pelagic animal, and is diagrammatically represented by Fig. 6. The larva has a

large oval anterior end, and a somewhat funnel-shaped posterior part. In the centre of the head-region lie two eye specks, and under this the beginnings of the brain. The middle of the animal is encircled by a band of ciliated cells which form the locomotor apparatus. Just beneath this band, or where the band is double within it, is the large mouth opening. The oesophagus is short and leads into the large mesenteron, and from this runs posteriorly the proctodæum to end in the anus. Beneath the mouth, and lying between it and the anus, is a bilateral plate of cells which is to form the nervous system. In the earliest stages the Trochophore represents a single segment —

furnish sufficiently good grounds for rejecting such a theory as exceedingly improbable.

First, I must insist upon the fact that those characteristics which the Pantopod-larva has in common with the Trochophore are only those features which any two Arthropods have as common characteristics of the first three segments; or, if we go further and include the Annelids, we may say which any two Articulates possess as common characteristics. They are these: a brain and ventral chord, united by commissures around the œsophagus; serial appendages corresponding in number to the number of segments; a digestive tract with stomodæum, mesenteron; and — and here lies the difficulty: not a trace of proctodæum does the Pantopod-larva possess, while both Nauplius and Trochophore have the digestive tract open posteriorly. In the young Pantopod-larva we have, so far as it goes, a fully formed and presumably functional digestive apparatus, and no reasonable account can, I believe, be given to explain how this posterior opening could have become lost in the transition of Trochophore into Pantopod-larva as Dohrn has supposed. If it be urged that in the young form the anus may have become functionless, and hence not developed, it will not mend matters, since we have every reason to believe that in the adult Pycnogonid the proctodæum is to a large extent useless.¹

I think these facts must prejudice us strongly against the position taken by Dohrn; but let us go further and examine into the other features of the Pantopod-larva.

¹ It has been suggested that it may serve for purposes of respiration, but no evidence for this is forthcoming.

acted upon in an increased degree, there seems every reason to believe that the young may have been much more acted upon and suffered far greater changes.

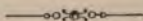
On the other hand, when we see in such a group as the Vertebrates that in the higher forms the young have been removed to a large extent from the action of surrounding conditions, — as, for instance, by being enclosed within a shell as in the Sauropsida, or retained within the uterus in mammals, — then can we understand why the young resemble each other more closely than do the adults, for the obvious reason that the adults have had to adapt themselves to more numerous external conditions while the embryo has remained fixed.

Indeed this may be pushed a step further, it seems to me, and explain why such young retain the characteristics of lower forms while the adults have lost such structures. This may be due to the young having been removed to a greater extent than the adults from a process of active selection. Hence in such a group, when we say that the Ontogeny tends to repeat the Phylogeny, we mean that the embryos have retained more of the ancestral features than have the adults.

But in such groups as the ones we are discussing, — Annelids, Crustacea, etc., — we ought to expect, if what I have said be true, the reverse of what we find in such a group as the higher vertebrates; viz. that the young forms diverge far apart, and the adults come nearer together.

This will tell strongly against the position taken by Hoek (also against the Nauplius theory), and render unnecessary or even improbable that we need bring together such forms as the Trochophore of the Annelids

EIGHTH LECTURE.



ON CARYOKINESIS.

By S. WATASE.

It has been said that one of the greatest discoveries of modern times is the generalization that all animals, however complex their structure, arise by the division and subdivision of a single, nucleated cell. The Cell doctrine in its original form, which had its origin in the comparative study of adult tissues, appears in a new light when viewed from the standpoint of the embryological history of these tissues, arising as they do, as the direct products of egg-cleavage, each segment being the exact copy of the original egg-cell, in so far as its general, superficial features are concerned.

Here arise two important problems : —

- (1) How does one egg, which is a single nucleated cell, and which gives rise to one animal, differ from another which gives rise to an entirely different organism ?
 - (2) What is the essential method of cleavage by which an apparently homogeneous ovum becomes converted into a complicated organism ?
- The first problem is well-nigh beyond the range of the present means of research. Take an egg of a star-

ference of form, always indicates difference of material substance." This doctrine of "Form and Matter," or of "Mechanism and Function," as expressed in the language of physiology, is the basis of our biological inquiries. As is clearly expressed in the words of Professor Burdon Sanderson, we must assume that "*every appreciable difference of structure corresponds to a difference of function*"; and conversely, each endowment of a living organ must be explained, if explained at all, as springing from its structure"; or in short, "*living material acts by virtue of its structure*, provided we allow the term structure to be used in a sense which carries it beyond the limits of anatomical investigation, *i.e.* beyond the knowledge which can be attained either by the scalpel or the microscope." Given protoplasm of definite structure, and we have its definite function or property. Or conversely, we observe a certain property in a given mass of protoplasm and we regard it as springing from a definite structure. When structure varies, the function must vary also; and when we observe certain peculiar properties we must ascribe them to peculiarities in structure.

One rational answer to our first inquiry is possible, viz. the protoplasmic structure of the egg which gives rise to one organism, must differ from that of the egg which gives rise to another different organism, the differences between the two being relatively as great as those which the two adult organisms display in their anatomical relationships.

If the similarities of two organisms must be attributed to the corresponding similarities of the protoplasm of the fertilized ova from which they respectively arise,

manner that one of the new nuclei by its division gives rise to the right, and the other to the left side of the adult organism. In another case, it has been maintained, the first division of the nucleus distributes the nuclear substance into future ectoderm and entoderm. And again, the formation of a certain organ, or of a system of tissues, has been traced in a most definite manner to a particular cell or group of cells in an early stage of cleavage. The more carefully the phenomena are studied, the more astonishing is the regularity and the precision with which the cleavage process is conducted and the differentiation of tissues is accomplished.

The occurrence of variations or irregularities in the mode of cleavage in a certain animal — irregularities as judged by the arrangement of the superficial cytoplasmic furrows — does not invalidate the importance of the conclusion which can be derived from the study of forms where absolute regularity prevails. For the essential feature of the cleavage process is the division and distribution of the nuclear substance of the ovum, and in so far as the nuclear substance is distributed in such a manner as to produce a symmetry of growth in the developing organism, it is immaterial whether its total quantity be divided exactly in two equal halves and distributed into right and left at the first cleavage, or whether it be divided into dissimilar portions and the equilibrium of growth be gradually secured during the subsequent stages of cleavage. The distribution of the nuclear substance may have been just as accurate and precise in one case as in the other.

A comparative study of cleavage of different ova affords another example illustrating this point. For

It is now quite generally conceded that the nucleus of the fertilized ovum contains all the hereditary characteristics of the parent organisms. It is this substance in the ovum which stamps the particular characteristics upon an organism of a given species. The study of fertilization has clearly demonstrated the metamorphosis of the sperm-nucleus into a constituent part of the cleavage-nucleus, and thence it is distributed to all nuclei formed in the subsequent cleavages. Morphologically, all the hereditary characteristics which the infant organisms inherit from the parents, must be traced back to a certain number of chromosomes which come from the sperm and egg-nuclei of the fertilized ovum. By cleavage, the potential characteristics become gradually analyzed into their special attributes—the attributes which we assign to different tissues of the larval or the adult organism. If, therefore, I may use one word to characterize the whole process of cleavage of the ovum, the term *Analysis* will perhaps best express our interpretation of the phenomenon. It is true, that we know very little as to the essential respects in which the nuclear substance in the entodermic cleavage sphere differs from the similar substance in the ectodermic sphere. In the present state of our knowledge on this subject, we can only infer a structural difference of the protoplasm from the careful study of the fate of the respective segments. If, for instance, one cell gives rise to a sense-organ, the fundamental molecular structure of that cell must be different from another which contains all the germs of an excretory organ, just as we are forced to conclude that the ova of different organisms are of necessity different, even if they appear

as to the method of analysis employed in such a process.

Such a *method* we find in *Caryokinesis*.

I will, therefore, describe the process which may be termed the mechanics of nuclear division, as based on my observation on Cephalopods and Echinoderms.

It is now agreed by many foremost investigators of the subject that the essential feature of caryokinesis lies in the division of the chromatic substance of the nucleus among the daughter cells, and the complicated system of spindle-rays is the mechanism to effect such a division. The development of a spindle clearly shows this, and the following is an attempt towards a further confirmation of the current view on the subject, as held especially by E. van Beneden and T. Boveri. In one important respect my view is entirely different from that of these authors, but this difference lies more in the interpretation of phenomena than in the facts themselves.

First of all, I will endeavor to describe the anatomy of a well-developed caryokinetic figure in the Cephalopod egg, upon which my observations have been chiefly carried on. The question of nomenclature presents some difficulty. I will use here a set of terms of a simple descriptive character, descriptive of either of function, of origin, or of topographic relationship of different parts. Since scientific nomenclature embodies marks of the progress of our knowledge on the subject, I will use, wherever convenient, such terms as have been introduced quite recently, and represent, in a measure, the latest phase of our information on the subject.

The accompanying illustration (Fig. 1) shows a caryokinetic figure in the blastoderm of the squid.

like, radiating structures. The former corresponds to the outline of the original nucleus, as will be shown later, and the latter constitute the *asters* of Fol, *spheres attractive* of van Beneden, or, to use a more recent nomenclature, the *archoplasmic spheres* of Boveri. The central area of archoplasm (*A*), is situated in the substance of

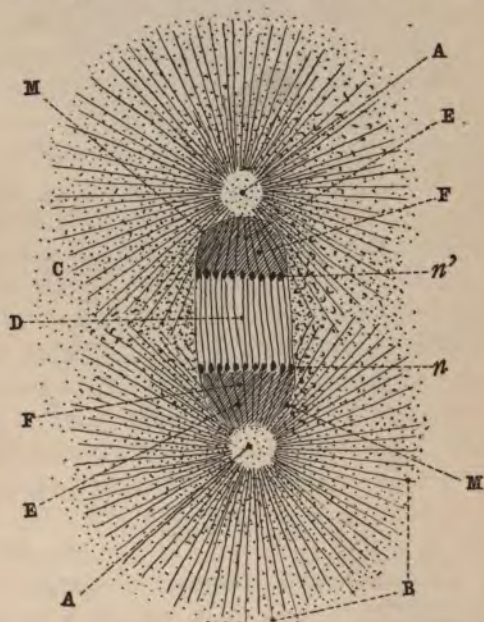


FIG. 2. — Asterias.

the *cytoplasm* (*C*). From the granular archoplasmic substance as a centre, there radiate out in all directions a large number of fibre-like rays, the *archoplasmic filaments* (*B* and *E*). A portion of these ray-fibres penetrate into the elliptical part of the figure, and constitute

nucleus. This polar flattening of the nucleus goes on until the nucleus presents the appearance shown in Fig. 4.

Space only forbids the illustration of the further changes, but it may be easily imagined that when this flattening of the nucleus is continued, the whole solid contents of the nucleus are reduced to a single flat sheet

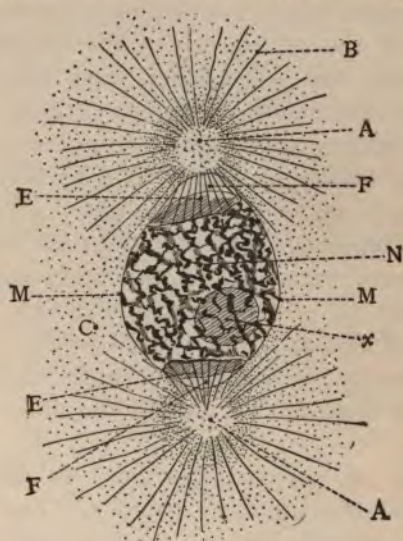


FIG. 3. — *Loligo*.

N Nucleus. *x* Nucleolus (?)

as it were, as shown in Fig. 5, forming the equatorial chromatic "plate." The spindle then, as its history clearly indicates, consists of two cones with their bases turned toward each other, and with their apices in the archoplasmic centres, as was first pointed out by van Beneden.

Boveri meets this difficulty by denying the filamentous nature of the interzonal substance, holding that what appears as filamentous is the optical expression of the longitudinal folds produced by the contraction of the two antagonistic groups of archoplasmic fibrils, whose distal extremities are fastened to the chromosomes. Strasburger ascribes to the substance the function of a wedge which grows in size by the absorption of the cytoplasmic fluid, and pushes apart the parallel "plates" of chromosomes. Platner explains the filamentous appearance of the interzonal substance as the optical expression of a protoplasmic stream. The existence of such a stream in a living dividing cell has, however, been denied by Strasburger.

As to the filamentous nature of the interzonal substance, there can be no question, as several observers have abundantly shown. My own studies on Cephalopods and Echinoderms have convinced me of the truth of this conclusion. Further, no optical difference could be observed between the archoplasmic fibrils at the poles of the spindle and the filamentous bodies in the intermediate zone, which fact has already been pointed out by several investigators.

Observing, then, that the interzonal portion of the caryokinetic figure consists of the bundle of filamentous substance, that this filamentous substance is essentially the same as the archoplasmic filaments of the spindle, that the length of these filaments is exactly the same as the space between the parallel bands of chromosomes in all stages, that the archoplasmic filaments have been growing in length from the poles toward the equator of the nucleus, and, further, that the interzonal filaments

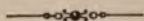
the latter will be carried by the former at its tip, and will be pushed forward as long as the filament continues to grow. Two opposing systems of the archoplasmic filaments behaving in a similar way, and lengthening in a contrary direction, would reduce the spherical nucleus first to a bi-concave disc, then to a flat "plate," and finally, into two parallel "plates," each "plate" traveling in an opposite direction. The interzonal filaments, then, according to this view, are the actual continuations of the archoplasmic filaments; but, instead of consisting of a single system, as at either end of the spindle, they are composed of two systems each dovetailing with the other, and growing in contrary directions. *Interzonal filaments* are, therefore, the prolongations of the *intra-nuclear filaments*. I am further inclined to believe that a certain optical peculiarity of the interzonal region, as, for instance, its aversion to take stains, is due to the existence in it of a proportionally large number of non-stainable archoplasmic filaments.

Having briefly sketched the general outline of the process by which the characteristic shape of a caryokinetic figure originates, it would be appropriate to devote a few words to the obscure point as to the origin and movement of the archoplasm itself. But as a matter of fact, we know as yet very little in regard to the origin of the archoplasm, sometimes with a definite body in its centre—the *centrosome*. A great authority like van Beneden looks upon it as a permanent organ of the cell, equal in value to the nucleus itself; but the whole question of its origin and its apparent homologues, which pass by different names in different cells, is too complicated and obscure to be discussed in this place.

most carefully studied by several investigators. At first the two daughter spheres lie in close opposition, later they separate more and more widely. As each sphere has a system of radiating filaments, there is formed a little spindle (Fig. 6, *S*) where they come into contact. This spindle lies outside of the nucleus, and has nothing to do with the larger one which has been described already. The daughter archoplasmic spheres migrate further apart, and finally settle themselves on the opposite sides of the nucleus. Their effect on the latter is soon seen. That surface of the nucleus upon which the archoplasm rests soon shows signs of flattening, as was shown in Fig. 3. This polar flattening of the nucleus has been interpreted as due to the pressure exerted by the growing archoplasmic filaments. The growth of the filaments continues, and the effects it produces upon the nucleus, in the arrangement and distribution of the chromosomes have already been described. Compare in this connection the series of stages shown in Figs. 3, 4, 5, and 1.

The above is a sketch of the mechanics involved in the distribution of the nuclear substance in the dividing cell. The history of the formation of the spindle has been briefly given, and the mode of its activity has been suggested. The spindle, however, plays only a part in the production of the caryokinetic phenomena. The whole behavior of the chromosomes preparatory to division, such as the transformation from a resting condition to a coil stage, followed by the longitudinal splitting of each filament, — phenomena which take place independently of the influence of the spindle, — has received no consideration, and, so far as I can see,

NINTH LECTURE.¹



THE EAR OF MAN:

ITS PAST, PRESENT AND FUTURE.

By HOWARD AYERS.

THE study of the human ear, its structure and its functions, is not alone a *modern* endeavor on the part of man to "know" himself; for history tells us, that the Greek philosophers and anatomists sought, both by dissection and physiological experimentation, to ascertain the anatomy of the organ, and how it is that we hear by the ear. The extent of their knowledge we do not know, for most of their anatomical treatises are lost to us.

Empedocles, 473 years B.C., referred the perception of sound to the cochlea; and Aristotle (384 B.C.) was acquainted not only with the internal ear of the higher vertebrates, but with that of fishes as well.

The Egyptian school of anatomists does not seem to have progressed beyond the knowledge borrowed from the Greeks.

¹ The memoir, of which this lecture is an abstract, will be issued in the *Journal of Morphology*, Vol. IV., No. 3.

possible the comparison of the embryonic conditions with the adult, and the establishing of important phylogenetic conclusions based on these relations.

John Beard first clearly saw the relation existing between the sense-organs on the surface of the body and the organ enclosed within the head by the formation of the auditory vesicle (the auditory labyrinth of the adult), but he failed to apprehend the *nature* of the involution and the relation of the sense organ to its walls.

E. P. Allis, by giving us the first thorough investigation of the relations of the sense-organs of the lateral line system to the surface of the body, in the account of which he describes the method of their enclosure within canals, the laws of their increase, and of the fusion and division of canals, the process of their sinking below the surface of the body, and of their enclosure within the cartilage (or the bone) of the skeleton,—made known the developmental plan according to which not only the superficial canal sense-organs grow and reach their adult relations, but also, as it is now discovered, the plan according to which the *ear sense-organ* divides and forms its canals and other parts. This latter fact is demonstrated by the published results of numerous embryological investigations on animals from the several classes of vertebrates.

In order that we may fully recognize the influence these investigations have had on the solution of the problems concerning the phylogenetic history of the human internal ear, it will be necessary first of all to understand the anatomy of the ear in some type form. For this reason I ask your forbearance while I briefly de-

Leaving out of consideration all other developmental processes connected with the completion of the auditory organ, such as its enclosure in mesodermic tissue which solidifies to form the ear-capsule (the bony labyrinth of the adult ear of higher forms), I wish to call your attention to two points of great importance for the correct understanding of the morphology of the ear.

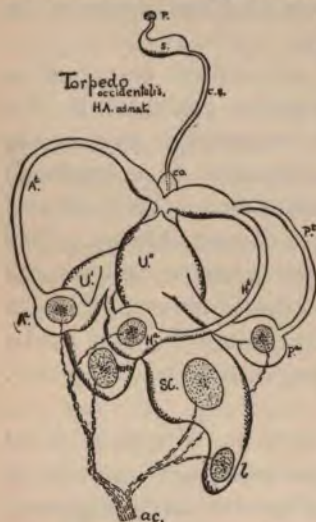


FIG. 1. — The left internal ear of *Torpedo occidentalis* dissected out of its cartilaginous capsule, and viewed from the outside. The somewhat diagrammatic figure represents the ear about twice its natural size, as found in a fish five feet in length.

- A^a* Anterior ampulla.
- A^t* Anterior canal.
- ac* Auditory nerve.
- c.e* Endolymphatic canal.
- co* Utriculo-sacculus cone.
- H^a* External ampulla.
- H^t* External canal.
- mu* Macula utriculi duct.
- l* Lagena and papilla lagenæ.
- P* Surface pore of endolymph canal; *s* its sac.
- P^a* Posterior ampulla.
- P^t* Posterior canal.
- SC* Sacculus and its macula sacculi.
- U* and *U'* Utriculus and utricle-sacculus chamber.

1st. The ear vesicle does not divide, as previous investigators have supposed, into superior and inferior portions, *but into an anterior and a posterior chamber.*

2d. The semicircular canals are not given off from the utricle alone, but from the *sacculus as well.* With these two misconceptions corrected, the way is clear which leads to the really simple-as-the-truth account of the morphology of the vertebrate ear, and we shall never again encounter an *auditory labyrinth.*

Each of these canals opens into the main sac of the ear by its two ends, though this usual relation is not adhered to by all vertebrates, since some of the cartilaginous fishes show the posterior canal separated almost completely from the main sac, communicating with it only by a small, much reduced canal, the two ends of the semicircular canal having been brought together and its two terminal openings fused into one.

In *Torpedo* the proximal (superior) ends of the canals (Fig. 1, near *co*), are brought together and empty into a common but very short tube, which serves to maintain the communication with the main sac. Before uniting, however, the external and posterior canals unite by communicating with a common *ama*,¹ while the anterior canal swells out into an *ama* of its own. There is no constancy in the relation of the ends of the canals to each other or to the main sac, and, as we shall see later on, the matter has no great morphological or physiological importance. The enlargements at the proximal ends of the canals are found among most of the lower forms and occur in the *development* of the higher groups, usually disappearing before maturity is reached. The distal (inferior) ends of the canals are swollen into globular bodies, the *ampullæ*, which are usually flattened on one side by the entrance of the nerve branch, which breaks up into a brush of fine fibrils as it enters the ampullar wall. The nerve fibrils are distributed to the sensory cells of the *crista acustica* or transverse ridge, which

¹ I shall call the superior terminal enlargements of the semicircular canals *amæ*, from the Greek *ama*,—a water-vessel,—since, unlike the *ampullæ* or the inferior terminal enlargements, they contain no nerve end organs and are mere fluid-holders. Their significance is unknown to us.

medium. This duct communicates with some of the sense-organ canals lying in the skin, and is innervated by one of their nerves.

The sense-organs, six in number, with perhaps a trace of a seventh, are placed, three in the ampullæ of the semicircular canals, as already described, these being designated the cristæ, while the other three are known as the maculæ and papillæ acusticæ; the one in the recessus utriculi, *U*, being the utricular macula *mu*, while the one in the saccular recess *SC* is called the macula acustica sacculi. It has budded off the lagenar spot, or papilla acustica lagenæ, *l*.

These organs are derived from the division of a single parent organ, as we shall see later, and hence their differences of form are secondary. The trunk of the auditory nerve (Fig. 1, *ac.*) is composed of two branches, each of which gives off three branchlets to the anterior and posterior divisions of the ear respectively. We may thus speak of an utricular and a saccular branch, each supplying the structures belonging to (*i.e.* developed from) its part of the ear. In *Torpedo* the anterior branch or the ramus utriculi gives off one branchlet to the crista of the anterior ampulla, another branchlet to the crista of the external ampulla, and a third to the macula utriculi. This latter branchlet is in reality composed of several branchlets; for the macula utriculi is a compound sense-organ, as the sequel will show.

The posterior or saccular branch gives off one branchlet to the crista of the posterior ampulla, a second branchlet to the macula sacculi, and a third to the papilla lagenæ, while there is possibly a fourth

lymphatic duct (*s*), and the duct itself into two quite symmetrical portions. The anterior corresponds to the anterior part of the Torpedo ear, and there is a similar correspondence between the posterior halves of these two ears. The main points of difference are, 1st, The sense-organs of the Myxine ear are only three in number, or at most four. 2d, The canals, only two in number, and they do not communicate by their amal ends with the main sac of the ear, or the utriculo-sacculus, for here the chambers are not separated though distinctly marked off. 3d, The endolymphatic duct does not communicate in the adult with the surface of the body.

The auditory nerve, however, has the same number of divisions, — two, — and they supply the utriculus with its anterior ampulla, and sacculus with its posterior ampulla, respectively, the same as in the Torpedo ear.

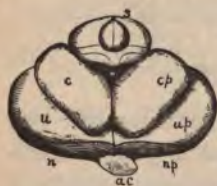


FIG. 3.—The right internal ear of a Lamper-eel (*Petromyzon fluviatilis*), viewed from its inner or cerebral face. The figure after Retzius.

- | | |
|------------------------------|-----------------------------------|
| <i>ac</i> Auditory nerve. | <i>u</i> Utriculus. |
| <i>c</i> Anterior canal. | <i>uap</i> Sacculus. |
| <i>cp</i> Posterior canal. | <i>s</i> Ductus et sacculus endo- |
| <i>n</i> Ramus utricularis. | lymphaticus. |
| <i>nap</i> Ramus saccularis. | |

In *Petromyzon* the ear is much more compact than in any other known form; the canals, though two in number and well developed, do not rise above the surface of the utriculo-sacculus; and although they fuse together at their proximal ends as in *Myxine*, they also open into the main sac by a short, small tube. The whole structure is divisible by a vertical passing through the apex and the middle of its base into anterior and

is very important, for it introduces us to a series of changes which have led to the production of the gnathostome type of ear.

The reptile, bird, and mammal ears furnish us with a progressive series in which the parts already present in the Torpedo are carried to successively higher degrees of perfection. The most noticeable change from the Torpedo condition is the much elongated lagenar region, or, as it is called in the mammalia, the cochlea, which by means of the high differentiation of its contained sense-organ has risen to first rank among the auditory sense-organs.

The utricular and saccular regions are relatively much reduced. The semicircular canals have undergone a similar reduction, and among the birds and mammals appear more nearly semicircular or more evenly curved than in either the reptiles or the fishes.

All of these ears retain traces of the primitive division into anterior and posterior chambers, and the relation of the nerves described for the *Cyclostome* and the Torpedo obtains throughout the group, except, of course, where a given sense-organ has divided, when, as is frequently the case among the higher types, two or more nerve branchlets are present where only one existed in the lower type.

In Fig. 6, which is a figure of the developing human ear seen from the outside, the anterior and external ampullæ are intimately related to each other and to the utriculus *U*, while the posterior is given off from the sacculus. A line passed through the space between *U* and *S* of the figure, and continued so as to pass out just above the ampulla of the posterior canal, divides the ear

general surface depressions the sense-organs sink down forming, as they do so, small pits, at the bottom of which the organ lies. The lips of the pit grow upward and inward, and meeting above arch over the pit forming the beginning of a canal. This arch grows away from the pit in two directions until it meets another canal, with which it fuses, or until its energy is spent, when it comes to a standstill and remains a longer or shorter canal open at both ends, possessing somewhere near the middle of its course the canal sense-organ which gave the first impulse to the development of the canal. The sense-organ lies in a pit which represents what we know in the ear canals as the ampulla. The lateral line sense-organs are then supplied with, or lie in, ampullæ.

The canals being formed in short sections, one to each sense-organ, and fusing as they do to make longer canals, we should expect the compound canal at the point of fusion of its two components would retain a pore connection with the surface from which the canals were formed. Such is the case.

Again, in the division of a canal organ and its canal, we should expect to find the canal retaining its surface communication by means of a single pore, if the division did not progress to completion, and we find this occurs regularly in the development of canals. The reverse of this process also occurs, in which the pore divides first, while the parent canal may remain undivided.

We shall see later on that the ear canals fuse and retain their communication with the surface by means of a single pore, and that in one instance a canal organ divides, bringing about an incomplete division of the original canal, so that both canal organs communicate

the study of the development of the internal ear than any vertebrate with which I am acquainted. Fig. 8 shows the auditory involution after it has assumed the saucer-shape already alluded to. This condition is the result of a concomitant thickening and sinking of the ectoderm, which over the area of the saucer represents one of the canal sense-organs of the lateral line system, and the whole process from the beginning on is but a



FIG. 8.—The head of an embryo Shark (*Acanthias vulgaris*), from nature, magnified 20 times. The figure shows the saucer-shaped depression containing the insinking sense-organ which is to be converted into the auditory sense-organs of the Shark.

- a.v* Auditory saucer (vesicle).
- ep* Epiphysis.
- f* Fore-brain.
- g* Gill region.
- h* { Upper and lower hind-brain region.
- h'* {
- m* Mid-brain.

repetition of the formation of the canal organ and its canal, as seen in *Amia*. As the saucer-shaped thickening sinks below the surface, the opening on the surface grows smaller, the bottom of the saucer increases in size, and the resulting structure is an auditory vesicle distinctly flask-shaped (Fig. 9, *a.v*). The neck of the flask grows longer, and finally appears bent backwards and inwards, owing to the increase in size of the head in this region, which causes a transla-

then drawn out in an antero-posterior direction. During this process the anterior end comes to point outward, while the posterior end is directed inwards toward the median line. There may now be seen several changes in the shape of the vesicle which, while not conspicuous, are very important, since they usher in a succession of transformations which ultimately produce the three



FIG. 11.—The ear of a very young Rabbit embryo, 11 mm. long. Figure after Krause.

- a* Anterior canal.
- am* Ampulla.
- d* Ductus endolymphaticus.
- l* Lagena.
- s* Sacculus.
- u* Utriculus.



FIG. 12.—The internal ear of a somewhat older Pig embryo, 33 mm. long. Figure after Krause.

- a* Anterior canal.
- am* Ampulla.
- d* Ductus endolymphaticus.
- l* Lagena.
- p* Posterior canal.
- s* Sacculus.
- u* Utriculus.

semicircular canals and the rudiment of the cochlea. These changes are visible on the outer and upper faces of the vesicle as slight ridge-like elevations of the surface, and on the posterior ventral end of the vesicle as a knob-like prominence (Fig. 10, *c*, *ch*, and *a.v*). Of the former there are two, of the latter a single one. The

quadrangular shape. This condition is found in embryos of three and a half to four weeks. The utricular and saccular divisions are readily distinguished, and even now the semicircular canals have begun to differentiate by the formation of two shallow depressions in the walls of the utriculus. Both the pocket common to the vertical canals and the pocket for the external canal are present. Below the latter is seen the larger and deeper evagination for the cochlea. When the embryo has reached the length of 8 mm., the cochlea has so far developed as to stand out distinctly from the sacculus, and is at the same time bent (Fig. 11, 1). At both ends of the common pocket of the verticals, and at one end (anterior) of the external depressions, are slight enlargements — the future ampullæ. From now on, the parts rapidly acquire individuality. The anterior canal is completed first. Then the posterior becomes cut off, and soon after the external is perfected.

The whole vesicle undergoes a marked change in form during this period, for, owing to the growth of the ductus endolymphaticus from the apex of the primitive vesicle, and the great elongation of the cochlear tube from the bottom of the saccular region, the canal complex now appears drawn out in a dorso-ventral direction. The cochlear canal has now, about the fifth week, one half a spiral turn, and a long groove has appeared on the inside of its wall (fold on the outside), from which the nerve end-organ — Corti's organ — arises. In the embryo of 30 mm. (Fig. 6) length the canals are well formed, and the ampullæ are quite prominent. The two verticals which from *their mode of development have up to this time occupied the same plane*, now begin

sense-organs of the auditory complex and of their canals. It is the morphological value of that sense-organ which, ever since its discovery by Retzius, has been such a source of discussion and investigation; viz. the macula acustica neglecta, supposed by some to belong to the utricle; by others, to the sacculus in the older sense.

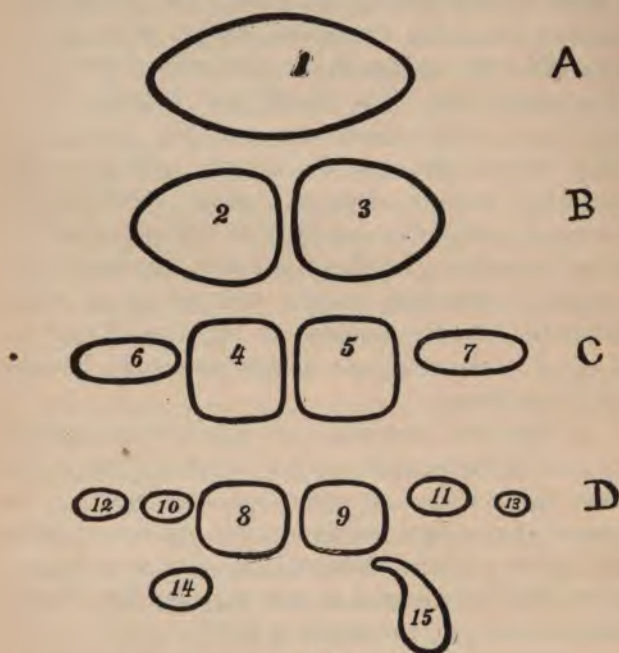


FIG. 14.

- A* Auditory vesicle.
- B* Utriculo-sacculus.
- C* Utriculo-sacculus + two ampullary canals.
- D* Utriculo-sacculus + two ampullary canals and lagenar canal.

Stage A represents the undivided superficial sense-organ of the vertebrate ancestor, as it is invaginated from the surface and enclosed within the

living vertebrate. And it is quite possible that the auditory saucer may contain the rudiments of the two primary sense-organs of the Cyclostome ear. The parent sense-organ soon divides transversely into two nearly equal parts, which are the anterior and posterior sense-organs respectively. The auditory vesicle is at the same time partly separated into two chambers (incomplete canals) to accommodate them. These chambers are the utricle and saccus.

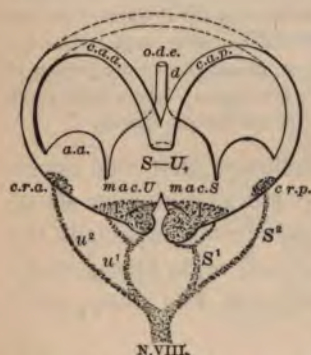


FIG. 15.— The Cyclostome type ear shown here is a very simple structure as compared with the complicated organ found among the *Gnathostomata*, but compared with its ancestral condition, *i.e.* the auditory vesicle, it is seen to have gone through many changes, and stands to-day midway between its earliest condition and the highest differentiation known. This diagram is constructed on the basis of the anatomy of the only two known forms of this group, *Myxine* and *Petro-*

myzon. The canals and their organs retain a very primitive condition of structure.

- caa* Anterior canal.
cap Posterior canal.
cr. a Crista acustica anterior.
cr. p Crista acustica posterior.
d Endolymphatic duct.
u.s The utriculo-sacculus.
u 1 and *2* Branchlets of the utricular branch of the auditory nerve.
s 1 and *2* The saccular branches of the same.

- ode* Terminal portion of the endolymphatic duct, which in neither of these Cyclostomes opens on the surface of the body in adult life.
mac. u Macula acustica utriculi.
mac. s Macula acustica sacculi.
1 and *2* The portions (1) of the sense-organs that remain in the parent cavity and the portion (2) which migrate into the recessus utriculi and lagena respectively.

Each of the two sense-organs of the second generation after a while divides into two unequal parts in such

The sense-organ numbered six in the Cyclostome stage (the crista acustica anterior, or anterior canal

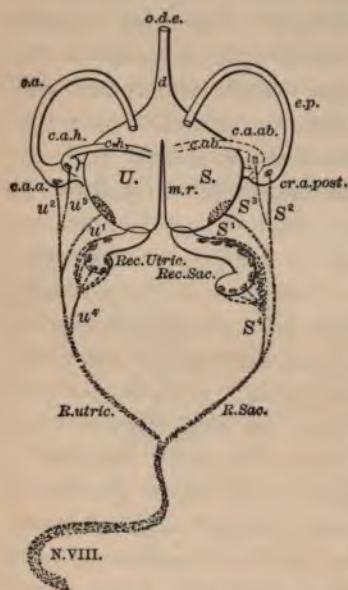


FIG. 16.—The Gnathostome type ear shown here illustrates the method and the extent of the modifications which the Cyclostome ear has suffered in its descent to this group. The anterior and posterior canal organs have each budded off an organ which, in the case of the anterior canal, produces a well-formed canal, the external, present in all the members of this group, while the posterior bud never produces a well-formed canal. The utricular recess, which contains a number of sense-organs derived from the division of the macula utriculi, is represented as forming a tubular prolongation of the utricular cavity, in order to more clearly show the parallelism of this group of organs with the lagenar group. In no known

form does the production of the canal proceed to the extent shown in the diagram. The sense-organs of the lagenar group are represented as separated from each other by an interval, whereas the actual relation in nature is much more intimate.

ca Anterior canal.
cp Posterior canal.
ch External canal.
c.ab Abortive canal.
u Utriculus.

rec. utric Recessus utriculi.
rec. sac Recessus sacculi.
d Ductus endolymphaticus.
s Sacculus.
o.de Orifice of the same.

organ, of *Myxine* and *Petromyzon*) has divided to produce sense-organs ten and twelve of the Gnathostome stage, *i.e.* the cristæ acusticæ anterior et horizontalis, of the human ear.

the nerve supply has been excluded from its just share in forming the conclusions.

These canal structures had no special phylogenetic significance for investigators in this field; for although it was known that the auditory vesicle was invaginated from the surface of the body, the connection of the sensory part of the invagination with the superficial canal organs was not understood. Now that we know that there is a genetic connection, many of the intricate problems receive their solutions, and the genetic relationships appear clear and certain for all the types. The demonstration of these facts deals another blow, and a fatal one, at the degeneration hypothesis which has been so persistently applied to the elucidation of Cyclostome anatomy and development, with such pernicious morphological results. (This will apply equally to *Amphioxus*, though only indirectly in this particular instance.) This solution relieves us from the necessity of explaining away the vertebrate ear on every occasion, when we seek to establish a relationship between the vertebrate and the invertebrate types; for we are led to see the value of very simple, superficial, sense-organs in an undifferentiated group of animals, for the building up of structures of great complexity, and of intricate relations to other parts of the animal body in the members of higher forms, and also to recognize the manner in which the structure and functions of organs may be profoundly changed in the course of time.

Now, while it is not known that *Amphioxus* is provided with an organ of hearing, the next higher forms do possess an internal ear of such structure that not only does it help us to understand the more complex

must be a genetic relationship between the canal organs of the internal ear and the superficial canal organs; and since there is not the slightest doubt that the superficial canal organs are the original or parent organs, we are brought to the unavoidable conclusion that the vertebrate internal ear is a transformed canal organ.

It follows from what I have said that the system of canal sense-organs must be a *very* ancient one, since it must have antedated the origin of the internal ear of the Cyclostomes.

Although *ontogenetic* evidence seems to lead to the conclusion that the auditory organ arose by the invagination of *a single superficial sense-organ*, it is by no means certain that this is true; for there are certain facts of comparative anatomy and certain phylogenetic considerations which point to the conclusion that the auditory organ has arisen by the bringing together of two originally distinct sense-organs which were together sunk below the surface. The main facts at present in favor of this view are these:—

1. In all eared vertebrates the auditory organ is supplied from two distinct brain centres, one lying in close connection with the facial nuclei, the other intimately related with the glossopharyngeal nucleus.

2. In all eared vertebrates the so-called auditory nerve is composed of two distinct roots—an anterior and a posterior—which supply the anterior and posterior chambers respectively.

3. In all these forms the anterior root is external to the brain, united with the facial nerve.

4. In some fishes the nerve to the posterior ampulla is derived from the glossopharyngeal nerve, between

the surface of the body midway between the roots of the facial and glossopharyngeal nerves as they issue from the brain. At the point of junction the two half-pores united into a single pore, which in some fish forms (*e.g.* Torpedo) persists as the outer opening of the endolymphatic duct, and the only persisting indication of the separate origin of these organs and their canals is their nerve supply. It is a necessary consequence of the great functional differentiation which the ear organs have suffered that their nerves should also become much increased in size, and instead of appearing now as *nerve branches* they have become really larger than the parent nerves from which they arose.

As a prelude to the little I have to say on the physiology of the internal ear, I wish to emphasize the following considerations: We have very slender foundation indeed for correctly judging of the functional relations of the integral parts of the internal ear, and what we have is largely speculative, based on our knowledge of the structure of the parts.

What we need at the present time is physiological experimentation. First of all, an extended series of varied, careful, and unbiassed experiments on the sense-organs of the lateral line system of the lower vertebrates, to determine their functions, and then more experiments on the internal ear of the least differentiated representatives of our type, to determine what functional modifications have arisen during the transformation processes. Finally, the combination of the knowledge thus gained, with the results of experiments upon the human subject.

followed by loss of the ability to equilibrate the body.

An extended presentation of the arguments for and against the equilibration theory of the semicircular canals would be too long and unprofitable to justify introducing it here, especially so now that there is no longer the slightest evidence in favor of the theory, since the results of experiments by the physiologist Steiner have been published. It is commonly stated that the auditory nerve, besides possessing the function of transmitting auditory impressions, also transmits stimuli to the equilibrious centre, and that the ampullæ of the semicircular canals contain the sense-organs which subserve this function.

The ampullar sense-organs may, however, be completely severed from their respective nerves without producing any disturbance in the equipoise of the body. The section of the ampullar nerves, even though the greatest care be taken to prevent damage to the connecting nerves, must produce an intense stimulation of the central end cells, and it is wholly unexplained why the ampullar nerves may be thus cut without producing any visible effect if the equilibration theory were true.

Experiments carried out in Hermann's laboratory in 1877, by Fraulein Tomaszewicz, showed that in bony fishes the semicircular canals and their ampullary sense-organs could be entirely removed without in the least influencing the equilibration of the body. Another set of experiments, even more decisive, were performed by Professor Steiner in 1888, in the physiological department of the Naples zoological station, on the

for it can be clearly shown that during the wounded state the bird is still able to equilibrate itself under certain conditions, and those conditions involve calling into use the tactile sense. The sensation of giddiness produced by injury to or destruction of the canals is due not to the injury of the ampullar sense-organs, but either to a disturbance of the centre of equilibration in the brain by mechanical injury to the cells of this centre, or to the cessation of the perceptions arising in part from the functional activity of the auditory mechanism. It has been observed that a pigeon operated on by canal section or destruction can, and usually does, steady itself and properly direct and execute coördinated movements, the moment its sense of sight is aided by the tactile sense sufficiently to enable it to form a correct judgment of its position in space and its relation to surrounding objects.

Now, barring nausea or other nervous disturbance accompanying section among the warm-blooded animals, it is plainly true that the animal's failure to coördinate its movements lies in the fact that it forms false judgments of its spacial relations on an insufficient basis sense-perception, the constant stream of auditory impressions having been cut off, even in the milder experiments, by the disturbance of the pressure equilibrium of the endolymphatic fluid.

On the basis of the evidence which had been produced by the advocates of this doctrine, Milne-Edwards disposed of the kinetic and statical theories of the equilibration functions of the semicircular canals in the following words: "Mais les hypotheses proposées

accessory apparatus is a ponderous mass, which only relatively powerful vibrations can set in motion. All vibrations of the air which do not succeed in moving this conducting apparatus are lost to us. It is for the purpose of making up this great loss that the external ear has been developed. Traces of accessory apparatus to place the internal ear in more favorable communication with the exterior, begin to make their appearance

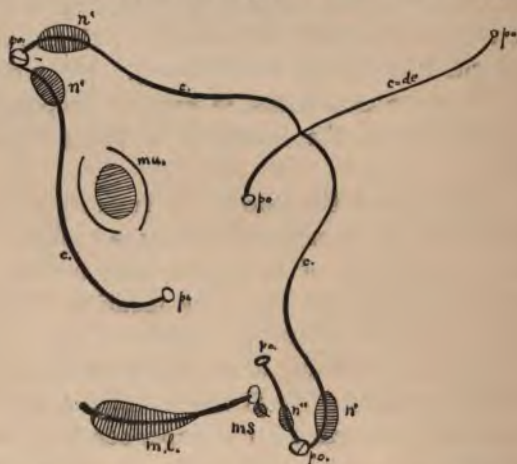


FIG. 17. — A projection of the internal ear on a flat surface, to illustrate the relations of the sense-organs and canals of the Torpedo ear, when the auditory chamber is brought to the surface and spread out flat.

c Canal.
po Canal pore.
n' Crista acustica.
mu Macula utriculi.

n'' Macula neglecta.
ml Papilla lagenæ.
ms Macula sacculi.
c. de Endolymphatic duct.

among the cartilaginous fishes, whose ears still retain their direct connection with the sea-water by means of an endolymphatic duct. This tendency is due to

In closing, allow me to recapitulate the more important features of oto-phylogeny, past, present, and to come.

In the PAST the ear of man was a canal organ of the lateral line system of sense-organs. A system which has disappeared from the surface of the adult human body; but which still occurs in a reduced condition during embryonic development. All its organs regularly produced protective canals, and the auditory organ came to differ from the neighboring organs merely in size and the greater depth of its ampullar pit. At first its functions were identical with those organs of the same system, having the same nerve supply; but as it was more and more removed from the surface of the body, it acquired greater protection against injuries and concomitantly greater sensitiveness. It increased in size and began the process of division, which has resulted in the organ as it exists at the present day.

These changes required untold millions of years for their perfection; for, since palæontological science tells us that this same *Amia* or ganoid Dog-fish which has retained its surface organs in such a primitive condition, existed in its present form, at the very least, twelve millions of years ago, you will readily conclude that the human mind can form no adequate conception of the period of time which elapsed since the ancestors of the Dog-fish were like the Cyclostome fishes in the structure of their ears.

For we know that at the present time *Amia* has an internal ear of greater complication than the *Torpedo*,

differentiation; it will, nevertheless, remain in the human descendants of the distant future, whatever their form may be, however keen or diversified their auditory function may become, merely A TRANSFORMED CANAL ORGAN.

thinking that the ancients not only knew of these currents but supposed them to be the essential features of the oceans.

While speaking of these older maps, I might add that there are many curious graphic attempts to explain the ocean currents. Among them the attempt of Vossius is noteworthy. His currents start from the interior of the globe, and after running their course, are taken back to mid-ocean (a safe place perhaps at that time because it was not likely to be investigated), and then they disappeared in a most remarkable series of mysterious whirlpools.

Twenty years after the discovery of America, Ponce de Leon, who had been Governor of Porto Rico, was replaced by Diego Colon. He set sail in 1513, with three vessels, to cross the straits between the Bahamas and Florida. While sailing south along the coast of Florida, they kept off shore to avoid shallows, and found themselves in a current against which they could not make headway even with a favorable wind. Their journals are very interesting at this point, because in them we have the first recorded descriptions of the Gulf Stream. Two of the vessels came to anchor, their cables "vibrating like musical strings," while it is recorded as a remarkable fact that the third vessel, being further off shore than the other two, failed to obtain an anchorage and "drifted out of sight in a clear day, with a fair wind."

The pilot of this expedition was Francisco de Alaminos, later on the pilot of Cortez. In his actions we have a fine example of the hardy character and practical nature of those early explorers. When the "Gold-land"

Albatross deserves an honorable place in connection with this work. There is, however, room for the more careful study of the relations of these currents, their changes under various meteorological conditions, and their effect upon the distribution of marine life. This has been the problem upon which we have been working for the past two seasons.

Let me now give a short outline of the course of a part of the North Atlantic currents. About two or three hundred miles west of the coast of Africa we find the first indications of the Equatorial current; this passes westward to the neighborhood of Cape St. Roque, where it divides, the portion in which we are interested passing northward. When this branch reaches the Windward Islands, it again divides, a part known as the Antilles current passing up to the eastward of these Islands; the main portion, however, under the name of the Carib current, passes westward between them. At this point Bartlett speaks of it not as a mere stream but a sea in motion. When this body of water reaches the straits between Yucatan and Cuba, its width is decreased to one-seventh of its former size, and its velocity doubled. At this point a small arm passes into the Gulf of Mexico, but the main current is deflected to the eastward by the banks to the north of Yucatan and passes out between Florida and Cuba as the Gulf Stream or Florida current.

The following table will give a more concise view of the character of the stream from this place onward and serve to give point to our discussion of it:—

over the various portions of the North Atlantic. A simple illustration of the way in which this effect is produced is obtained by placing the hand with the fingers together upon the table, and then forcibly moving it forward, when it will be found almost impossible to keep the fingers together; contact with opposing currents, also, tends to reduce the velocity and breaks the main band up into smaller bands.

I would call attention to the fact that this widening of the stream takes place upon its eastern side, the western edge being much sharper and better defined than the eastern. This is probably due to the position of the Labrador current between it and the coast. The line of contact between these two currents is so sharp that it can often be seen in the surface water from the deck of a vessel. During one of the late trips of the *Grampus*, I had a curious illustration of the fact, that under proper conditions the line of contact could be noticed in the dark. We were about forty miles south of Nantucket, and had just completed a set of observations upon one of our stations. We had a strong south-westerly tide, the air was so nearly quiet that we could just get headway enough to hold our course, and the temperature of the surface water was 67° F. We had scarcely gotten under way, when I noticed a distinct noise similar to that of a tide rip, about a mile ahead of us. I watched our approach to this noise with great interest, as I knew there were no tide rips in this portion of the ocean. We soon passed into the troubled water, which was producing this noise. Upon taking the temperature at this point I found it to be 72° F. We had passed from water flowing southwest to water

tor to go towards the pole, it passes from a region of great velocity of rotation to one where a lesser velocity is found, and consequently gradually drops back to the right or left, as the case may be. So, too, the water of the pole, as it moves towards the equator, is constantly advancing from a region of small velocity to a greater one, and consequently gains in longitude as it goes on.

Upon examination of any good map of the currents of the oceans, it will be found that they follow this law in their circuits without regard to the coast lines, though the coasts materially change their directions in many instances. This is particularly true of the southern portions of the Atlantic, Pacific, and Indian Oceans, where the courses of the currents are not interfered with by the land masses of the globe, and are perfectly free to move according to the law which controls them.

We shall now consider some of the causes of these currents, and the various theories which have been held concerning them. Magnetism and the moon have been a great source of comfort to people perplexed over the difficulties presented by some of the phenomena of nature. It was only recently that I saw an attempt to explain the currents by the use of the laws of magnetism.

Among the earliest explanations we have of these currents are those given by Kepler and Leonardo da Vinci. Kepler believed they were due to the rotation of the earth, while da Vinci thought they were caused by a disturbance of the thermal equilibrium at the equator. I will only take time to allude to one of the many curious explanations given by the older geographers of these currents. Vossius, whose map I have

warm water is simply an exchange brought about within narrow limits, and involves no other motion than that of conduction in a fluid. Besides, later observations by Forschhammer and Buchanan have shown us that these variations are not as important as they were supposed to be.

About the same time V. Schilling, a Russian, advanced a tidal wave theory. It is interesting only from the fact that it is exactly the reverse of the theory of Vossius. As the tidal wave passes around the equator, it produces a flood tide at that point, and consequently an ebb tide must be formed at the higher latitudes. Existing facts and the theory cannot be harmonized without straining both, and so it must be rejected.

There are two modern schools of theorists with regard to the causes of ocean currents.

I. Those who advocate a *thermic circulation* in explanation. This idea is defended by Schmid, Mubry, Carpenter, and Krummel. It is believed by this school that the differences in temperature between the tropics and the poles are sufficient to account for the currents. This belief is based largely upon an experiment of Carpenter's, in which the water at one end of a trough was cooled, whereas that at the other end was warmed. Small objects, such as pigment granules which floated and colored the water as they advanced, show a motion of a character tending to support this view. Mubry adds to this the idea that the motion is aided by the rotation of the earth.

The difficulties in the way of this theory are: first, that centrifugal motion does not do what it is supposed to, *i.e.* start a rotary current. I have already shown its

of their power, however, is found in the temporary reversal of the regular current of the North Indian Ocean during the period of the southwest monsoon.

It is not to be wondered at, then, that such a difficult problem as that of the ocean currents presents many dark and unsolved points. If I might suggest a theory, I would say that the winds are the prime mover, setting the current in motion, and all the other factors produce variations or aid this motion and quite likely retard it under the varying conditions in which they are found. The words of Humboldt are almost prophetic in this connection, but I very much doubt whether he had any definite conception of the fulness and completeness of his statement, when he said: "They (the currents) cannot be explained by any *one* assignable cause; the phenomena are complicated by the ebb and flow of the tides, the duration and force of the predominating winds, the density and specific gravity of the water, as modified by temperature in different latitudes, seasons, and depths of water."

Whatever may be their cause, we cannot help but wonder at some of the efforts produced by the constancy and power of these currents. I sometimes think a good way of seeing the benefit of any given order of things is to suppose them reversed. Suppose, for instance, that instead of having this continual circulation in the oceans, keeping every portion in a normal and proper condition for life, and blotting out all dangerous variations, our oceans were stagnant bodies of water. You will instantly recognize the effect which would be produced upon the life of the globe. These great currents have been aptly compared to the veins and arteries

ments of the currents, tides, winds, etc., all affect the changes which occur to such an extent, that they must be studied simultaneously and over a considerable area, and also during the various seasonal changes before any adequate idea can be obtained of even the limits of the problem.

The physical, mechanical, and chemical changes which take place are all the result of the operation of laws, which are so complicated in their action and interaction that their study in combination becomes an interesting as well as profitable occupation.

If some relation could be found to exist between the meteorological conditions upon the land (which are being constantly observed and discussed) and the changes which occur in the bodies of water, the information would be of the greatest service to our fishermen. It would prevent many fruitless searches for schools of fish in regions unfitted by the temperature of the water for the distribution of the food of these fishes, and consequently of the fish themselves. As the temperature of the water, doubtless, controls this distribution, a systematic study of the various causes of its changes, and the means by which they are brought about, becomes an eminently proper subject for investigation.

Thus a definite object has been kept in view in the prosecution of the physical inquiries of the Commission. This became necessary as the work of the Commission developed. At first it was quite right that the investigations should be experimental and tentative, and only as the problems assumed shape could some positive object be given to each research along definite lines, with the view of uniting the results into a studied

to study these changes and ascertain their law, if possible, in addition to the careful study of the biological problems otherwise involved.

Two such investigations are now being carried out by the Commission, one upon the ocean, and the other in Long Island Sound. A description of these will suffice to give an idea of the character of the physical work which is now being carried on, and its importance as an element in the study of this problem of making good a deficiency in such an essential food product, caused by the increased demands of our times, and intensified in its effect by the carelessness or thoughtlessness of our fishermen through ignorance and in some instances wilfulness in the pursuit of a merely temporary gain.

In order to give a practical and positive character to the investigation upon the ocean, the region between Nantucket Island on the east and Block Island on the west was taken, since it lies in the track of the schools of fish. After consideration, it was decided that a preliminary survey should be made to obtain some definite ideas upon the relations of the cold and warm currents, the changes which take place in their relations, the influence of the winds and other meteorological phenomena in producing these changes, and to notice any effect produced by the tides. The Fish Commission schooner *Grampus* was placed at my disposal, and outfitted with the proper apparatus and instruments, to carry out this work as an experiment, to see whether any results of interest could be obtained.

A series of lines 130 miles in length and at ten-mile (ten minutes of longitude) intervals from one another, were laid out between the two above-mentioned islands.

which the fish feed, is crossed and followed by the schools of fish. In this way the cold coast current is bridged over, so to speak, and the fish brought within reach of the fishing fleet. As the warm water approaches the coast, it seems to be broken up into bands, which lose their velocity by coming into contact with a current flowing in the opposite direction to that in which they originally moved, and their course is again modified to such an extent that they are found flowing in the opposite direction of the Gulf Stream. We have further gained concise ideas of the relations of the cold coast current and the warm waters of the Gulf Stream; and know something of the changes which take place in these relations through the mechanical influence of the winds. The outline of the problem has thus been obtained. The results were interesting enough to induce Professor Mendenhall, the superintendent of the Coast Survey, to coöperate with the commission in the study of these temperature problems; and this summer a still more extended investigation is in hand, in which the Coast Survey steamer *Blake* and the schooner *Grampus* are engaged. The work has progressed to such a point that I may say that we shall have over 375 stations to study, giving us over 4000 serial temperatures, 1000 specific gravity observations, and over 14,000 general meteorological records.

Last year the only means of comparison for our meteorological observations were the records made in New York and Boston; but this year we shall have in addition for this purpose a station upon the Nantucket New South Shoal light-ship, through the courtesy of the Light-house Board. Here a series of observations

action of the tides in that body of water do not carry any substance placed in it out to sea, but keep it moving back and forth until it is decomposed. This fact suggested the idea that possibly the oxygen in the water could not take care of any such excessive charge of poisonous nitrates and nitrites as would be developed by these decomposing substances.

The waters of the Sound are therefore being investigated this season with reference to their chemical condition at various depths. The currents are at the same time being carefully studied by a member of the Coast Survey, and it is hoped in this way to obtain a complete view of the physical conditions under which the oyster has been evidently forced to live.

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